Plant and Soil **46**, 473–486 (1977) Ms. 2969

RELATIVE GROWTH AND NUTRIENT ACCUMULATION RATES FOR TOBACCO*

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SUMMARY

Tobacco plants (*Nicotiana tabacum* L.) were grown from transplanting until floral expression in the phytotron units of Southeastern Plant Environment Laboratories to evaluate the relationship between relative growth rate (RGR) and relative accumulation rates (RAR) of N, P, K, Ca, and Mg. RAR is calculated to be analogous to RGR. Plants were grown in both controlled-environment rooms with artificial light and air-conditioned greenhouses with natural light at three temperature conditions and three application rates of N-P-K. RGR and RAR were calculated only for the period of grand growth which occurred within the interval from 7 to 32 days after transplanting.

In general, neither RGR nor RAR were affected by temperature or nutrient level. However, both temperature and nutrient level affected dry matter accumulation of the plants apparently by an influence on the rapidity with which plants adjusted to their new environment during the initial 7-day interval after transplanting. RAR for P and K were coequal with RGR of the whole plant; thus, the concentrations of P and K within the plant tended to remain constant during growth. RAR for N, Ca, and Mg were less than RGR for the whole plant; thus, internal concentrations of these nutrients declined

* Research reported in this paper was supported in part by National Science Foundation (RANN) Grants GI–39229 and GI–39230. Operation of the Phytotron Units of Southeastern Plant Environmental Laboratories at Duke and North Carolina State Universities was supported by National Science Foundation Grants GB–28950–1A and GI–28951. Approved as Paper Number **4773** of the Journal Series of the North Carolina Agricultural Experiment Station, Raleigh, NC.

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during growth. RAR of N, Ca, and Mg for the whole plant were equivalent to RGR of the roots. As a rationale for the association of RGR of roots and RAR of N, it is proposed that the soluble carbohydrate pool in the roots concurrently influences both N absorption, as NO_3^-, and growth of new roots of immature plants.

INTRODUCTION

Computer simulation models of plant growth and yield are invariably concerned with factors within the aerial environment, such as radiation, temperature, and carbon dioxide concentration, which delimit growth. Absorption and translocation of mineral nutrients also delimit growth. In recent publications models have been proposed for nitrogen uptake by cotton (*Gossypium hirsutum* L.) [12 13], for phosphorus uptake by onions (*Allium cepa* L.) [3 4 18] and lettuce (*Lactuca sativa* L.) [29], for potassium fluxes in roots of barley (*Hordium vulgare* L.) [20], and for calcium uptake by several species [16].

A concept common to these reports is that for long-term uptake of nutrients by whole plants the absorbing power of roots is independent of such plant growth components as relative growth rate (RGR) and net assimilation rate (NAR) only at low external concentrations. During the exponential growth period, when the greatest portion of mineral nutrients are accumulated in field culture, RGR and NAR are related to internal concentration for nutrients mobile within the plant, such as nitrogen, phosphorus, and potassium, but not for non-mobile nutrients, such as calcium [3 4 18]. The driving force for absorption of a nutrient at the root surface presumably responds to the changes in internal concentration of the nutrient (brought about by changes in growth rates) and is independent of the shoot to root ratio. The proposed plant-generated driving force for the absorbing power of roots is referred to as 'plant demand' [6 19]. Data from many sources [1 5 8 14 15 20] support the concept of plant demand within conditions of exponential growth and adequate external nutrient availability.

The uptake of non-mobile nutrients, such as calcium, while responsive to plant demand, would not be expected to be related to internal concentration. Whereas a mobile nutrient can be translocated to maintain growth during brief periods of reduced uptake, growth is dependent upon concurrent uptake of non-mobile nutrient [2 19]. Loneragan and Snowball [16] have proposed a relationship in which uptake rate of a non-mobile nutrient (calcium) per unit of

root weight is a proportional function of RGR and internal nutrient concentration but is dependent on the root to shoot ratio. It follows that if root to shoot ratio decreases during growth, internal concentration of nutrient would also decrease until such time as it becomes growth limiting.

Nitrogen uptake by plants should follow the general relationship proposed by Nye *et al*[18]. It clearly moves through the phloem [20] and thus can be considered as a mobile nutrient. Furthermore, data of Clarkson [6] indicate that the internal composition of nitrogen in 14-day old barley seedlings is independent of external supply. Above a critical external concentration, shoot weight and nitrogen composition were relatively constant, but below the critical external concentration, shoot weight was reduced while shoot nitrogen composition remained at the same, near constant level. Nevertheless, Jones *et al.*[12 13] note that nitrogen composition of cotton decreases with time. Since they accept the postulate of a plant demand toward a constant nitrogen composition if external supply is nonlimiting to uptake, and assume that this constant level is that characteristic of young seedlings, they conclude that the internal compositions typical for early growth represent a maximum and those typical for more mature plants represent a minimum required for growth. The difference between the maximum and minimum nitrogen compositions within any organ becomes a functional reserve to supply new growth when current uptake is less than demand. This concept is compatable with the conclusion of Pitman [20] that since nitrogen is translocated around the plant, the plant can act as its own source of nitrogen during exponential growth. Hence, he suggests that nitrogen is an exception to the plant demand concept of proportionality of growth and mobile nutrient accumulation.

This paper explores the feasibility of utilizing in a dynamic model of tobacco (*Nicotiana tabacum* L.) the concept that RGR of the plant regulates rate of nutrient accumulation. A second objective is to determine if the apportioning of nutrient ions among different plant organs is similarly regulated by RGR of the organs.

METHODS

Seeds of a flue-cured variety of tobacco (*Nicotiana tabacum* L. 'NC 2326') were sown onto the surface of sand filled plastic cups (5-cm square) and cover-

ed with fine quartz sand to a depth of not more than 2 mm. The cups were placed in an air conditioned greenhouse of the North Carolina State University (NCSU) phytotron unit of Southeastern Plant Environment Laboratory (SEPEL). A day/night temperature of 26/22 °C (± 0.5°C) was maintained for a 42-day period of seedling growth. The seedlings were watered 2 to 3 times a day with deionized water, and once a day with the medium nutrient solution listed in Table 1. At the end of the seedling growth period on 17 September when the plants had attained a total dry weight of about 1.5 g/plant and a total leaf area of about 200 cm^2/plant, half of the seedlings were taken to the Duke University Phytotron unit of SEPEL and half were retained at the NCSU unit. At each unit, the seedlings were transplanted into individual 25.4-cm diameter plastic pots filled with sand.

Separate controlled environment rooms (CERs) at both phytotrons were programmed for cool, warm, and hot temperatures of 22/18, 26/22, and 30/26°C (± 0.4°C). Each CER had a light intensity during the 9-h day period of 450 hlx from a combination of cool white fluorescent and incandescent lamps at an input wattage ratio of 10 : 3. Photosynthetically active radiation (PAR) was approximately 750 $\mu E\ m^{-2}\ sec^{-1}$, or about 140 cal $cm^{-2}\ day^{-1}$, as measured with a Lambda LI–1905 Quantum Sensor.* Light to dark transitions were abrubt. The 15-h dark period included a 3-h interruption by the incandescent lamps to establish long day floral photoperiods [31]. Insignificant PAR is contributed by the incandescent lamps. Relative humidity in the chambers was controlled to provide a vapor pressure deficit of approximately 5 mmHg at all temperatures [7]. In CERs at NCSU atmospheric concentration of CO_2 was maintained during the light period at a building ambient of 375 to 400 ppm [7]; however, CERs at Duke were not equipped for CO_2 control and CO_2 levels during the light period varied with plant growth from the building ambient of 350 ppm at transplanting to a minimum of about 200 ppm at final sampling [22].

Three air conditioned greenhouses were also used at each phytotron. Because the greenhouses must be shared with other experiments, identical temperatures could not be established at the two locations. At NCSU 22/18, 26/22, and 30/26°C, and at Duke 20/17, 26/23, and 29/26°C were used for the cool, warm, and hot temperatures. In addition, the greenhouses at NCSU had a 12-h day thermoperiod and those at Duke had an 8-h thermoperiod. At NCSU long day photoperiods were achieved by a 3-h interruption by incandescent light in the middle of the dark period; at Duke, the day photoperiod (but not thermoperiod) was extended to 16-h by incandescent light. The measured average daily total radiation in the greenhouses of both phytotrons during the growth period was 249 langleys. This is approximately equal to an average PAR of 190 cal $cm^{-2}\ day^{-1}$. Ambient CO_2 of 375 to 400 ppm was maintained in the greenhouses at NCSU. CO_2 was not controlled in the Duke green-

* Trade names are given as a part of the exact experimental conditions and not as an endorsement to the exclusion of other products that may also be suitable.

houses, but because of the large ratio in air volume to leaf area the CO_2 levels remained in a range of 300 to 350 ppm.

Immediately after transplanting, 45 plants were placed into each CER and greenhouse. All plants were watered in the forenoon and at noon with 600 ml of deionized water. This is approximately the volume of water retained at field capacity in the sand-filled pots. In the afternoon all pots were flushed with an excess of deionized water. After being allowed to return to field capacity, 600 ml of a nutrient solution were applied. Three nutrient solutions, in which concentrations of N, P, and K varied concurrently, were applied to different subsets of plants in each environment. The composition of these nutrient solutions is listed in Table 1.

TABLE 1

Macroelemental concentrations of nutrient solutions*

Solution	Macroelemental concentration (mM)						
	NO_3^-	$H_2PO_4^-$	K^+	Ca^{++}	Mg^{++}	Na^+	SO_4^{-2}
High	29.6	1.7	13.2	7.0	2.8	0.8	0.9
Medium	21.4	1.3	8.8	7.0	2.8	0.0	2.9
Low	14.3	0.8	5.9	7.0	2.8	0.0	5.2

* Concentrations of iron and micronutrients were the same for all three solutions and are listed by Raper [21].

A total of five harvests were taken for each treatment over a 6-week growth period. The harvests from CERs were at 0, 7, 14, 21, 31, and 42 days and from greenhouses at 0, 7, 14, 22, 32, and 43 days after transplanting. Three plants were taken from each treatment. Individual leaves were measured for calculation of areas [25]. The plants were separated into leaf, stalk, and root components, dried in a forced-air oven at 65°C, weighed, and analyzed for N, P, K, Ca and Mg by the Analytical Service Laboratory of the Department of Soil Science, NCSU.

The plants in all treatments had attained an advanced stage of floral development by the final sampling date. Growth or nutrient accumulation between 7 and 31 or 32 days after transplanting can be described by regression equations of the form

$$\ln W = a + b(t) \tag{1}$$

where W is a measured plant parameter, a is the intercept, b is the regression coefficient, and t is plant age in days after transplanting. The regression coefficient b for total plant dry weight is equivalent to the Relative Growth Rate (RGR) as defined by the relationship [9]

$$RGR = [\ln(W_2/W_1)]/(t_2 - t_1) \tag{2}$$

where W_2 and W_1 are dry weights at the end and beginning of the interval of time marked by t_2 and t_1. The values of RGR for whole plants (RGR_P) and

for the leaf, stalk, and root parts (RGR_L, RGR_S, RGR_R) have thus been calculated as b of Equation [1]. This same method was used to calculate values for relative rate of accumulation of N, P, K, Ca, and Mg in the whole plant and plant parts ($RARN_P$, $RARN_L$, $RARN_S$, $RARN_R$, $RARP_P$, etc.). Relative leaf area growth rate (RLGR) was also calculated. The correlation coefficients (r) for regression equations of all growth and nutrient accumulation components were significant at the .05 level of probability and all but six per cent were significant at the .01 level of probability.

Logarithmic growth responses during the initial 7-days sampling interval were not linearly related to time, although from past experiments [32] it is known that growth of seedlings on a logarithmic scale is linearly related to time during the interval immediately before transplanting. Since all plants within the current experiment represented a single population at transplanting ($t = 0$), the intercepts derived from Equation [1] can be used as indicators of the rapidity with which plants adjusted to an equilibrium with their post-transplant treatment. A positive increase in 'a' would indicate a more rapid adjustment to the steady-state rate for the treatment.

Before calculating the relative growth rates, the individual plant weights were averaged for the three plants per sample. These materials were then pooled within treatment and sampling date for inorganic analysis. For statistical comparison among the calculated rates, analyses of variance were performed using either nutrient solution or temperature as the treatment, and growth facility (*i.e.*, CER or greenhouse at NCSU or Duke) as replications. The h.s.d. of Tukey's multiple range procedure [30] was computed to compare mean response among treatments.

RESULTS AND DISCUSSION

The dry matter accumulation of the whole plant and plant parts and the total leaf area were affected by temperature and nutrient supply. Typical of the response is the measured plant performance at 31 (CERs) or 32 (greenhouses) days after transplanting (Table 2). A significant positive response to temperature for dry matter accumulation of the whole plant, leaves, and stalk occurred between the cool and warm temperatures. Conversely, dry matter accumulation by roots was reduced by the hot temperature. Effects of temperature on nutrient accumulation followed a pattern similar to that of dry matter. In general, plant response was positively related to external nutrient supply. An exception occurred for roots. Neither dry matter nor nitrogen content of the roots was affected by external nutrient supply.

The RGR for the whole plant did have a slight positive response between cool and warm temperatures (Table 3), but this limited

TABLE 2

Average dry matter and nutrient content of plants at 31 or 32 days after transplanting

Variable	Unit of variable	Temperature condition				Nutrient supply			
		Cool	Warm	Hot	h.s.d. (.05)	Low	Medium	High	h.s.d. (.05)
Whole plant									
Dry weight	g	54.5	79.8	73.9	12.0	61.3	68.7	78.1	12.0
N content	mg	1,522	2,097	2,056	353	1,502	1,962	2,213	255
P content	mg	231	308	295	40	226	280	329	27
K content	mg	2,331	2,985	2,969	365	1,971	2,792	3,523	322
Ca content	mg	684	1,057	980	268	842	960	866	n.s.
Mg content	mg	221	307	287	44	241	275	298	43
Leaves									
Area	dm^2	69.7	100.6	106.9	14.5	77.4	94.6	105.3	13.7
Dry weight	g	29.7	38.8	37.7	4.4	30.8	35.2	40.3	4.8
N content	mg	989	1,354	1,424	324	986	1,293	1,487	194
P content	mg	142	184	188	22	138	172	204	29
K content	mg	1,504	1,765	1,832	n.s.	1,190	1,729	2,124	242
Ca content	mg	578	821	799	210	683	792	717	n.s.
Mg content	mg	142	206	199	33	153	186	208	36
Stalk									
Dry weight	g	13.8	28.2	27.0	6.2	20.1	22.9	26.0	n.s.
N content	mg	302	544	486	106	328	476	509	115
P content	mg	51	93	85	19	61	79	90	21
K content	mg	551	986	963	174	614	852	1,034	153
Ca content	mg	70	142	142	26	112	129	114	n.s.
Mg content	mg	35	62	56	13	43	51	59	11
Roots									
Dry weight	g	11.0	12.8	9.1	2.6	10.4	10.7	11.7	n.s.
N content	mg	231	201	165	46	187	192	217	n.s.
P content	mg	38	31	23	9	27	30	36	6
K content	mg	284	207	174	91	174	211	278	89
Ca content	mg	41	41	38	n.s.	47	40	35	9
Mg content	mg	44	39	32	11	45	39	31	8

increase was almost entirely due to RGR of the stalk (RGR_S). External nutrient supply, which had significant and consistent effects on dry weights of whole plants at 31 or 32 days after transplanting, had no effect on RGR of either the whole plant or individual plant parts. The RAR for the various nutrients by the whole plant or plant parts were affected by neither temperature nor nutrient supply. Thus, the differences in plant responses measured at the con-

TABLE 3

Relative growth and nutrient accumulation rates calculated as the regression coefficient 'b' of Equation [1], for the growth interval of 7 to 32 days after transplanting

Variable	Units of variable	Temperature condition				Nutrient supply			
		Cool	Warm	Hot	h.s.d. (.05)	Low	Medium	High	h.s.d. (.05)
Whole plant									
RGR_P	g	0.122	0.129	0.129	0.007	0.124	0.127	0.129	n.s.
$RARN_P$	mg	0.113	0.115	0.113	n.s.	0.113	0.115	0.111	n.s.
$RARP_P$	mg	0.129	0.127	0.124	n.s.	0.129	0.129	0.124	n.s.
$RARK_P$	mg	0.127	0.122	0.122	n.s.	0.124	0.124	0.124	n.s.
$RARCa_P$	mg	0.113	0.117	0.115	n.s.	0.117	0.120	0.106	n.s.
$RARMg_P$	mg	0.115	0.120	0.117	n.s.	0.117	0.122	0.115	n.s.
h.s.d.(.05)		0.009	0.009	0.009		0.009	0.007	0.009	
Leaves									
RLGR	dm^2	0.113	0.117	0.117	n.s.	0.117	0.117	0.115	n.s.
RGR_L	g	0.113	0.115	0.117	n.s.	0.115	0.115	0.115	n.s.
$RARN_L$	mg	0.108	0.108	0.106	n.s.	0.108	0.108	0.106	n.s.
$RARP_L$	mg	0.122	0.120	0.117	n.s.	0.122	0.120	0.115	n.s.
$RARK_L$	mg	0.122	0.117	0.115	0.005	0.120	0.117	0.117	n.s.
$RARCa_L$	mg	0.111	0.113	0.111	n.s.	0.115	0.115	0.104	0.009
$RARMg_L$	mg	0.115	0.120	0.115	n.s.	0.117	0.120	0.111	n.s.
h.s.d.(.05)		0.009	0.009	0.009		0.009	0.009	0.007	
Stalk									
RGR_S	g	0.166	0.186	0.184	0.007	0.180	0.177	0.182	n.s.
$RARN_S$	mg	0.166	0.175	0.168	n.s.	0.173	0.173	0.164	n.s.
$RARP_S$	mg	0.175	0.180	0.177	n.s.	0.177	0.180	0.175	n.s.
$RARK_S$	mg	0.159	0.166	0.164	n.s.	0.164	0.164	0.161	n.s.
$RARCa_S$	mg	0.164	0.173	0.168	n.s.	0.166	0.173	0.166	n.s.
$RARMg_S$	mg	0.145	0.168	0.164	n.s.	0.152	0.159	0.164	0.007
h.s.d.(.05)		0.016	0.014	0.012		0.016	0.016	0.016	
Roots									
RGR_R	g	0.117	0.115	0.113	n.s.	0.113	0.117	0.117	n.s.
$RARN_R$	mg	0.101	0.090	0.092	n.s.	0.094	0.094	0.094	n.s.
$RARP_R$	mg	0.117	0.099	0.101	0.014	0.106	0.108	0.104	n.s.
$RARK_R$	mg	0.101	0.085	0.090	0.012	0.090	0.092	0.094	n.s.
$RARCa_R$	mg	0.111	0.097	0.104	n.s.	0.106	0.108	0.097	n.s.
$RARMg_R$	mg	0.099	0.090	0.094	n.s.	0.097	0.104	0.088	0.014
h.s.d.(.05)		0.009	0.009	0.009		0.009	0.007	0.009	

TABLE 4

'a' values fitted with Equation [1]

Variable	Units of variable	Temperature condition				Nutrient supply			
		Cool	Warm	Hot	h.s.d. (.05)	Low	Medium	High	h.s.d. (.05)
Whole plant									
Dry weight	g	0.196	0.371	0.343	n.s.	0.219	0.290	0.398	n.s.
N content	mg	1.600	4.216	4.237	0.260	3.924	4.101	4.331	0.175
P content	mg	1.552	1.960	1.973	0.246	1.589	1.808	2.088	0.198
K content	mg	3.942	4.354	4.373	0.260	3.914	4.260	4.488	0.168
Ca content	mg	3.102	3.406	3.419	0.283	3.173	3.251	3.502	0.263
Mg content	mg	1.858	2.116	2.130	n.s.	1.953	1.934	2.215	n.s.
Leaves									
Area	dm^2	0.788	1.135	1.172	0.260	0.870	1.036	1.186	0.120
Dry weight	g	−0.062	0.152	0.117	0.198	−0.055	0.065	0.193	0.141
N content	mg	3.675	4.023	4.073	0.265	3.703	3.910	4.152	0.226
P content	mg	1.310	1.715	1.771	0.316	1.333	1.598	1.865	0.235
K content	mg	3.629	4.073	4.106	0.350	3.592	3.984	4.230	0.136
Ca content	mg	3.016	3.330	3.348	0.249	3.086	3.185	3.426	0.223
Mg content	mg	1.504	1.782	1.867	n.s.	1.538	1.639	1.971	0.214
Stalk									
Dry weight	g	−2.623	−2.418	−2.333	n.s.	−2.570	−2.422	−2.381	n.s.
N content	mg	0.661	1.002	1.080	0.260	0.587	0.891	1.262	0.251
P content	mg	−1.412	−0.891	−0.845	0.336	−1.264	−1.098	−0.845	0.313
K content	mg	1.476	1.966	2.045	0.424	1.513	1.861	2.102	0.203
Ca content	mg	−0.857	−0.306	−0.120	0.470	−0.419	−0.463	−0.396	n.s.
Mg content	mg	−1.128	−1.045	−0.983	n.s.	−1.057	−1.091	−1.011	n.s.
Roots									
Dry weight	g	−1.365	−1.144	−1.255	n.s.	−1.206	−1.322	−1.239	n.s.
N content	mg	2.307	2.600	2.314	n.s.	2.328	2.399	2.498	n.s.
P content	mg	0.039	0.454	0.164	0.272	0.101	0.173	0.385	0.281
K content	mg	2.415	2.786	2.604	0.283	2.464	2.632	2.715	0.240
Ca content	mg	0.329	0.774	0.451	0.373	0.580	0.403	0.562	n.s.
Mg content	mg	0.541	0.797	0.484	0.295	0.776	0.357	0.656	0.299

clusion of the 7 to 32 day growth interval for both temperature and nutrient supply (Table 2) must be attributable to the growth activity while the plants were adjusting to a new equilibrium with their environment during the initial 7-day period after transplanting. Although this experiment lacks the necessary detailed sampling during this initital period to support a definitive conclusion, one can speculate that the plants placed into the warm or hot temperatures reach-

ed their new growth and nutrient uptake equilibrium more rapidly than plants placed in the cool temperatures. A similar lag in rate of morphological development occurs for shifts in temperature [26]. This conclusion is in line with the 'a' values of Table 4. The pattern of lower 'a' values for dry weights and nutrient contents at the low temperature and two lower nutrient supplies correspond to the pattern of lower dry matter and nutrient contents (Table 2).

Two inferences can be drawn from these relationships. Firstly, a change in ambient temperature has a more pronounced effect on plant growth and nutrient accumulation than does temperature per se. Secondly, a high initial external concentration of nutrient is more important for obtaining maximum growth of plants than is the external concentration once the plant has adjusted to its environment.

During the 7 to 32 day growth interval, both $RARP_P$ and $RARK_P$ were equal to RGR_P regardless of temperature or external nutrient supply (Table 3). Hence, in agreement with the plant demand concept for regulation of rate of uptake, the percentage composition of these elements tended to remain constant. From these results, it can be concluded that after an initial period of adjustment, rate of uptake of phosphorus and potassium can be included in a dynamic model of tobacco growth as a function of plant growth.

Conversely, $RARN_P$, $RARCa_P$, and $RARMg_P$ were lower than RGR_P. Consequently, the percentage composition of these elements within the whole plant progressively decreased as the plant mass increased. Uptake rate of these elements cannot be considered to be regulated directly by plant demand or those environmental factors which regulate growth rate of the whole plant. Rather, since $RARN_P$, $RARNCa_P$, and $RARMg_P$ correspond to RGR_R, it appears that uptake rate of these nutrients is linked with factors affecting rate of root growth. This was expected for calcium [16] which, since it is absorbed in the apical regions of roots [10 28], would predictably have an uptake rate proportional to growth rate of roots of an immature plant. However, the relationship between $RARN_P$ and RGR_P is contradictory to models proposed for uptake rate of nitrogen [12 13]. Since increased external supply of nitrogen failed to change the equilibrium $RARN_P$, these results do not concur with the assumption that the observed decline in plant composition of nitrogen with age is a function of insufficient external supply [12 13]. Although these

data do not refute the suggestion [20] that the plant demand for nitrogen is modified by the ability of the plant to act as its own source of nitrogen by internal translocation, they do offer empirical evidence that rate of nitrogen uptake is coequal with rate of root growth.

The observed relationship between $RARN_P$ and RGR_R agrees with the conclusion by Jackson *et al.* [11] that the nitrate uptake (the only ion of nitrogen used in this experiment) is at least partially controlled by the concommitant translocation of photosynthate to the roots. (Although active uptake of phosphorus and potassium also require energy expenditure, there is no evidence of a requirement for concommitant availability of carbohydrate.) For a model being developed for tobacco growth (M. Wann, C. D. Raper, Jr., and H. L. Lucas, unpublished), experimental evidence supports the assumption that flow of photosynthate within the plant follows the hierarchy of leaves, stalk, and roots such that photosynthate is available for root growth only after requirements have been met for growth of leaves and stalk and maintenance respiration for existing leaf, stalk, and root mass. Under conditions favorable for photosynthate flow to the roots, only a small pool of soluble carbohydrates (5 to 7% of dry weight) is maintained in the roots with most of the available photosynthate being immediately committed to growth-respiration and nonmobile 'grown' materials [27]. Thus, if it is presumed that soluble carbohydrate reserves necessary to facilitate absorption of nitrate [11 17] are transitory in roots and must be utilized concurrently with utilization of carbohydrate for root growth, the rate of nitrogen uptake would be equivalent to rate of root growth. For an immature and actively growing plant, RGR_R is generally lower than RGR_P (Table 3) and imposition of environmental conditions which restrict photosynthesis exaggerate this difference [24 32]. Thus, $RARN_P$ would also be lower than RGR_P with the resultant occurrence of progressively declining percentage composition of nitrogen in the plant.

The observations of RGR_P, $RARN_P$, $RARP_P$, $RARK_P$, and $RARCa_P$ of this experiment can be compared with analogous growth and nutrient accumulation components derived from field data [23]. During the interval of grand growth from 21 to 49 days after transplanting, RGR of plant tops (leaves plus stalk) was 0.122 g g^{-1} day^{-1}. This compares with an average RGR_P from Table 3 of 0.127 g g^{-1} day^{-1}. RARP and RARK for field plants were 0.120 and 0.117

mg mg^{-1} day^{-1} which can be considered to be equal to the RGR. RARN and RARCa were 0.106 and 0.108 mg mg^{-1} day^{-1} for the field-grown plants, less than the RGR. The field experiment was conducted in a season with adequate, evenly distributed and non-leaching rainfall and without abrupt temperature changes; thus, these data represent plant growth relatively unaffected by lag periods which could alter the relationships. They do offer evidence that, if the effects of lag periods can be assessed, the general relationship among RGR and RAR observed in phytotron culture can be applied to field conditions.

Changes in RGR for the three organ groups were accompanied by directional, but not proportional, changes in RAR for the various nutrients. This is demonstrated by calculating the ratio of $\overline{RAR}$ to $\overline{RGR}$ for the plant parts (Table 5). With the exception of nitrogen,

TABLE 5

Ratio of $\overline{RAR}$ to $\overline{RGR}$, $\overline{RAR}$ for each nutrient and $\overline{RGR}$ are the means for Table 3

	Nutrient				
Plant organ group	N	P	K	Ca	Mg
Whole plant	0.89	1.00	0.98	0.91	0.93
Leaves	0.93	1.04	1.03	0.97	1.01
Stalk	0.95	0.99	0.91	0.94	0.88
Roots	0.82	0.92	0.80	0.90	0.82

the ratio declines with the hierarchial ranking of leaves, stalk, and roots. This decline in ratio is most pronounced for potassium and magnesium. Hence, the apportioning of nutrient elements among plant parts do not follow the same fluxes as dry matter.

ACKNOWLEDGEMENTS

We thank Emory York for his assistance with plant culture, Dr. M. E. Watson and his staff for inorganic analysis, Directors of the phytotrons Drs. R. J. Downs and H. Hellmers for the cooperation of their staffs, and Dr. W. A. Jackson for comments during preparation of the manuscript.

Received 29 September 1975

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