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Competition among Individual Plants in Crop Population

IV. Growth analysis from the viewpoint of root behavior*

Yukio KUJIRA and Mikio KANDA

(*Institute of Agricultural Research, Tohoku University, Sendai 980*)

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The growth analysis which was introduced by WATSON[8] and his collaborates was a method dealing with the plant growth only in relation to total plant weight and plant top characters. They have rarely mentioned about root characters and the quantitative interrelation between top and root. We were considered more essential that plant growth should be discussed not only from responses of above ground parts of plant to spatial environmental conditions but also from the aspects of several characters of root behavior and top-root relationship. Some attempts on the quantitative growth analysis from the viewpoint of root behavior were made by WELBANK[10] and HACKETT[1], using the specific absorption rate of nitrogen and root surface area. The approach of this kind, however, has been left unexplored because of the difficulties of the quantitative measurement for the root characters.

In the previous papers[4,5], we have tried to ascertain whether or not α-naphtylamine (α-NA) oxidizing activity in roots which indicates the respiratory activity in roots can be used as one of indices for the plant growth. So, we studied about the quantitative relationship between α-NA oxidizing activity (root capacity) and root dry weight. We have pointed out that root dry weight was closely related with the α-NA capacity, and was expressed as the linear function of α-NA oxidizing activity (α-NA capacity[5]), so that the total plant dry weight showed as the following mathematical expression;

$$\mathrm{Pw} = f(\mathrm{T/R\ ratio}) \times f(\alpha\text{-NA capacity}),$$

where Pw is plant dry weight.

In this paper, we tried to extend the plant growth analysis from the viewpoint of root behavior using 3 factors, i.e. α-NA oxidizing activity (α-NA capacity), relationship between top and root and the distribution of dry matter produced.

Materials and methods

Materials used were *Lolium multifrorum* LAM., mammos italian B *sp.* as erect type and mammos A *sp.* as weeping type. The experiment was carried out in a greenhouse from May to August in 1975, by water culture with HEWITT's solution[2].

Three planting densities, 3 cm×3 cm:D (3), 6 cm×6 cm:D(6), 9 cm×9 cm:D(9), and two nutrition levels, 1/2 (NO_3-N:50 ppm) and 1/10 (NO_3-N:10 ppm) Hewitt's solution, were used as the treatments in the experiment. The particular experimental methods were the same as described in the previous report[5].

Results

1. *Unit root activity (URA)*

α-NA oxidizing activity in roots per hour per unit root dry weight was calculated as the quotient of α-NA oxidizing activity per plant per hour divided by total root dry weight. We call this quotient unit root activity (abbreviated as URA). $\overline{\mathrm{URA}}$ value over each period among successive samplings in advance with plant age was shown in Fig. 1. The values were calculated by the following equation,

$$\mathrm{URA} = \frac{\mathrm{Ra}}{\mathrm{Rw}} = \frac{\mathrm{d\ ln\ Rw}}{\mathrm{d\ Rw}} \cdot \frac{\mathrm{d\ Ra}}{\mathrm{d\ ln\ Ra}},$$

$$\simeq \frac{\Delta\ \mathrm{ln\ Rw}}{\Delta\ \mathrm{Rw}} \cdot \frac{\Delta\ \mathrm{Ra}}{\Delta\ \mathrm{ln\ Ra}},$$

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$$\therefore \overline{URA}=\frac{\ln Rw_2-\ln Rw_1}{Rw_2-Rw_1}\cdot\frac{Ra_2-Ra_1}{\ln Ra_2-\ln Ra_1}$$

where Ra is root activity (α-NA oxidizing activity in roots/hr), Rw is root dry weight.

$\overline{URA}$ decreased gradually as time elapsed, and there was no remarkable difference of $\overline{URA}$ between nutrition levels, though the difference of the value between planting densities was recognized. Throughout the experimental period, $\overline{URA}$'s in high planting density were always higher than those in low planting density, i.e. D(3) > D(6) > D(9).

2. *Root weight ratio* (*RWR*)

The ratio of the root dry weight (Rw) to total plant dry weight (Pw), i.e. root weight ratio (abbreviated as RWR) proposed by WELBANK[10], is given by the expression,

$$Rw/Pw=RWR.$$

Then,

$$T/R \text{ ratio}=Tw/Rw=(Pw-Rw)/Rw$$
$$=\frac{1}{X}-1 \text{ (where } Rw/Pw=x).$$

The RWR value is recognized as a measure of the distribution of dry matter produced by photosynthetic systems of plant between roots and tops. Calculated $\overline{RWR}$ over each period between successive samplings were shown in Fig. 2. The values were calculated by the following equation,

$$RWR=\frac{Rw}{Pw}=\frac{d\ln Pw}{d\,Pw}\cdot\frac{d\,Rw}{d\ln Rw}$$
$$\simeq\frac{\Delta\ln Pw}{\Delta Pw}\cdot\frac{\Delta Rw}{\Delta\ln Rw}$$

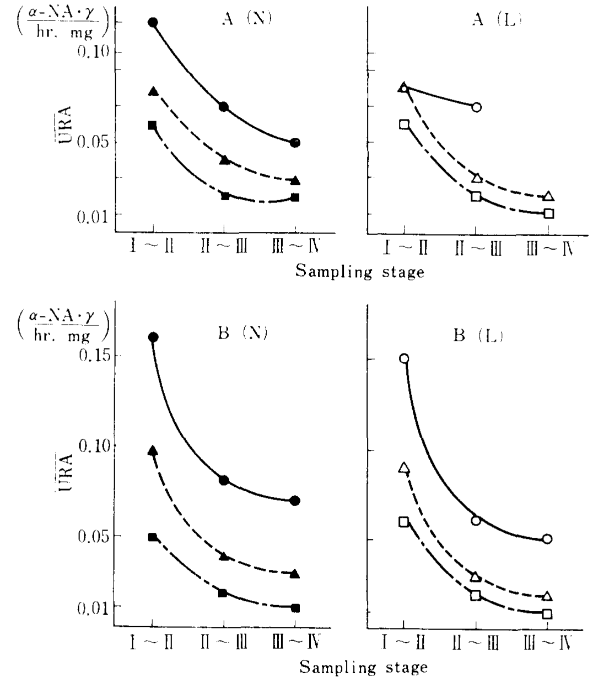

Fig. 1. Changes in the $\overline{URA}$ in relation to plant age for different nutrition levels, planting densities and plant types.

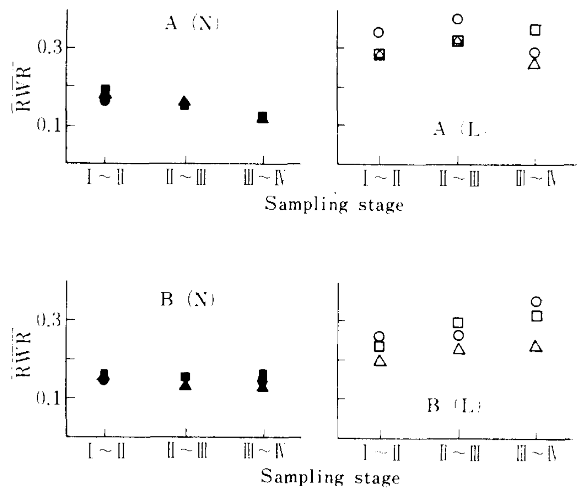

Fig. 2 Changes in the $\overline{RWR}$ in relation to the plant age for different nutrition levels, planting densities and plant types.

Note (1)

●: Density (3 cm × 3 cm), Nutrition (NO_3-N: 50 ppm)
▲: D. (6 cm × 6 cm), N. (〃)
■: D. (9 cm × 9 cm), N. (〃)
○: D. (3 cm × 3 cm), N. (NO_3-N: 10 ppm)
△: D. (6 cm × 6 cm), N. (〃)
□: D. (9 cm × 9 cm), N. (〃)

Note (2)

A: *Lolium multifrorum* LAM., A *sp.* (weeping type)
B: 〃 B *sp.* (erect type)

Note (3) Sampling stage, I, II, III, IV, represent 9/VII, 24/VII, 6/VIII, 13/VIII, respectively.

$$\therefore\ \overline{RWR}=\frac{\ln Pw_2-\ln Pw_1}{Pw_2-Pw_1}\cdot\frac{Rw_2-Rw_1}{\ln Rw_2-\ln Rw_1}$$

where Pw is plant dry weight, Rw is root dry weight.

There was little difference of $\overline{RWR}$ between planting densities under the condition of high nutrition level, a considerable difference, however, in low nutrition level. Discussing about the nutrition levels, $\overline{RWR}$ became larger with the nutrition level was lowered irrespective of the planting densities.

3. *Root assimilation rate (RAR)*

Increasing rate of total plant dry weight per unit α-NA oxidizing activity in roots is named root assimilation rate (abbreviated as RAR) by us, that is shown by the following expression.

The relationship between plant dry weight (Pw) and α-NA oxidizing activity in roots per hour (Ra) was shown by the next expression,

$$Pw=c+d\,Ra \quad \cdots\cdots(1),$$

where c and d are constant.

From (1),

$$d\,Pw=d\cdot d\,Ra \quad \cdots\cdots(2)$$

$$RAR=\frac{1}{Ra}\cdot\frac{dPw}{dt} \quad \cdots\cdots(3)$$

$$\overline{RAR}=\frac{1}{t_2-t_1}\int_{t_1}^{t_2} RAR\ dt$$

$$=\frac{1}{t_2-t_1}\int_{t_1}^{t_2}\frac{1}{Ra}\cdot\frac{d\,Pw}{dt}dt$$

$$=\frac{1}{t_2-t_1}\int_{t_1}^{t_2}\frac{d\,Pw}{Ra}$$

$$=\frac{d}{t_2-t_1}\int_{Ra_1}^{Ra_2}\frac{d\,Ra}{Ra} \quad \text{(from (2))}$$

$$=\frac{d\,(\ln Ra_2-\ln Ra_1)}{t_2-t_1} \quad \cdots\cdots(4)$$

from (1)

$$d=\frac{Pw_2-Pw_1}{Ra_2-Ra_1} \quad \cdots\cdots(5)$$

from (4) and (5),

therefore

$$\overline{RAR}=\frac{\ln Ra_2-\ln Ra_1}{Ra_2-Ra_1}\cdot\frac{Pw_2-Pw_1}{t_2-t_1}.$$

Calculated $\overline{RAR}$ over the period among successive samplings was shown in Fig. 3. There was the tendency of the decrease in $\overline{RAR}$ value in accordance to the increase of

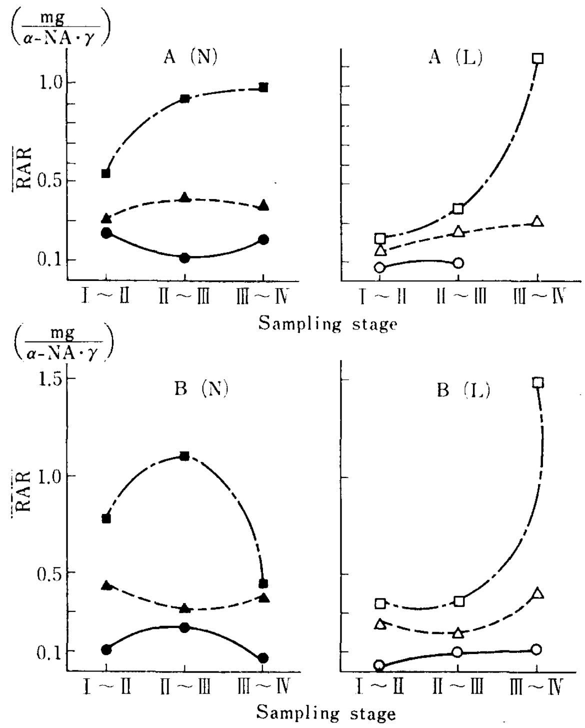

Fig. 3. Changes in the $\overline{RAR}$ over each period among successive samplings with advance of growth stage for different nutrition levels, planting densities and plant types.

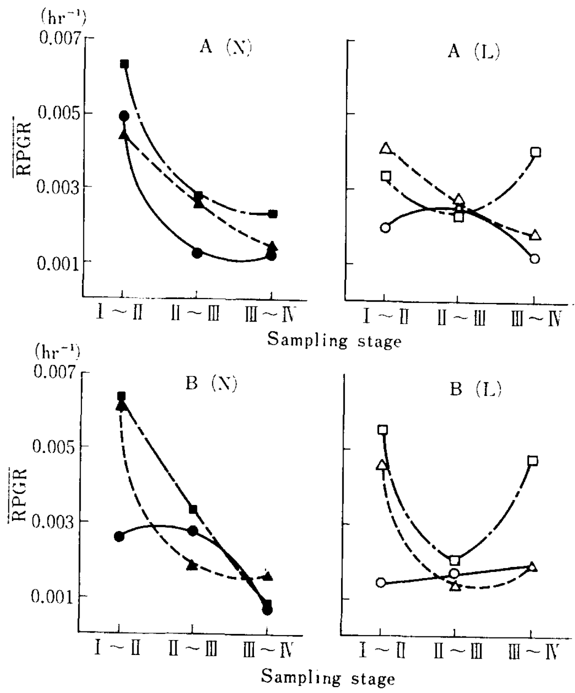

Fig. 4. Changes in the $\overline{RPGR}$ over each period among successive samplings with advance of growth stage for different nutrition levels, planting densities and plant types.

planting density, as D(9)>D(6)>D(3), and the difference of $\overline{RAR}$ value among planting densities increased as time elapsed. Discussing about the standpoint of nutrition levels, the value of $\overline{RAR}$ were smaller in low nutrition level (NO_3-N : 10 ppm), though the $\overline{RAR}$'s in low density (9 cm×9 cm) in low nutrition level was shown extremely high value more than those in high nutrition level in the later stage of experimental period.

4. *Relative plant growth rate* (*RPGR*)

The relative growth rate of total plant dry weight was expressed in the following mathematical expression,

$$RPGR=\frac{1}{Pw}\cdot\frac{d\,Pw}{dt} \cdots\cdots\cdots\cdots\cdots (1)$$

The increase of total plant dry weight in each short period between successive samplings was reasonably assumed to be fitted the exponential equation,

$$Pw=Pw_0\cdot e^{\alpha t}\ (Pw_0 \text{ is constant}).$$

So that mean RPGR's ($\overline{RPGR}$) over each period among successive samplings were calculated from the following equation based on the above assumption, and the relationship between $\overline{RPGR}$ and plant age (t) was shown in Fig. 4.

$$\overline{RPGR}=\frac{1}{t_2-t_1}\int_{t_1}^{t_2} RPGR\,dt,$$

where Pw is plant dry weight,

$$\overline{RPGR}=\frac{1}{t_2-t_1}\int_{t_1}^{t_2}\frac{1}{Pw}\cdot\frac{d\,Pw}{dt}dt$$
$$=\frac{1}{t_2-t_1}\int_{Pw_1}^{Pw_2}\frac{d\,Pw}{Pw} \quad (\text{from } (1))$$
$$=\frac{\ln Pw_2-\ln Pw_1}{t_2-t_1}.$$

$\overline{RPGR}$ decreased as time elapsed, and there was the tendency that $\overline{RPGR}$ value increased with the decrease of planting density, as D(9)>D(6)>D(3). There seemed to be that $\overline{RPGR}$'s in low nutrition level (NO_3-N:10 ppm) were always smaller than those in high nutrition level (NO_3-N:50 ppm) throughout the experimental period. $\overline{RPGR}$ in D(9), however, jumped up markedly at the later stage of the experimental period in low nutrition level, although the tendency has not been verified whether or not it was ordinary one.

5. *Root growth analysis from the viewpoint of root behavior*

Considering the relative total plant growth rate, based on the above mentioned concepts, it can be expressed by the following equation.

$$\frac{1}{Pw}\cdot\frac{d\,Pw}{dt}=\frac{\text{Root activity}}{Rw}\times\frac{Rw}{Pw}\times\frac{1}{\text{Root activity}}\cdot\frac{d\,Pw}{dt}$$

where Pw is total plant dry weight, Rw is root dry weight, root activity is α-NA oxidizing activity in roots per hour.

In this manner, relative total plant growth rate can be divided into 3 factors which are connected with root behavior as follows;

$$(RPGR)=(URA)\times(RWR)\times(RAR).$$

Discussion

The method for plant growth analysis was developed by WATSON[8,9] and others, VERNON[12] and others, HUGHES[3] and others, WHITEHEAD[11] and others, based on the leaf area as assimilative structures which concerned with photosynthesis, and among various growth functions the most basic expression of the so called growth analysis in the mathematical expression is;

$$\frac{1}{W}\cdot\frac{dw}{dt}=\frac{1}{L}\cdot\frac{dw}{dt}\times\frac{L}{W}$$

or $(RGR)=(NAR)\times(LAR)$

where W is plant dry weight, L is leaf area, t is growth stage (time).

The total plant dry weight is the sum of top dry weight and root dry weight, and, as a matter of course, water and all sorts of minerals of nutrition elements were absorbed by root system and translocated into upper part of the plant through the mediation of the physiological root functions.

It is necessary to be considered that plant growth must be dealt in connection with the top-root relationships and physiological activities in root.

We proposed a new idea that the relative plant growth rate was shown as the product of 3 factors, URA (unit root activity), RWR (root weight ratio) and RAR (root assimilation rate). As was already mentioned, RPGR in low planting density was larger than in high planting density (Fig. 4).

Discussing this results obtained from this experiment in connection with the above stated 3 factors, $\overline{URA}$ was higher in high planting density than in low planting density, but total plant dry weight and root dry weight in low planting density were larger than in high planting density. $\overline{RAR}$ value in low planting density, which supported by the greater total plant dry weight, was larger than in high planting density. As a consequence, it follows that $\overline{PRGR}$ in low planting density was larger than in high planting density. $\overline{RPGR}$ value decreased with the decreasing nutrition level (NO_3-N). As nutrition level decreased, root's RGR became larger than top's RGR, and $\overline{RWR}$ in low nutrition level became larger than in high nutrition level. The relative importance of root dry weight as to the contribution to making up the total plant dry weight became larger than that of top dry weight because of the increased $\overline{RWR}$ value without decrease in $\overline{URA}$ value as nutrition level decreased. In consequence, total root activity per plant increased in low nutrition level.

The increasing rate of top dry weight in low nutrition level decreased more than in high nutrition level owing to the increase of $\overline{RWR}$ in low nutrition level, so that $\overline{RAR}$ value decreased in low nutrition level. The phenomenon, that $\overline{RPGR}$ decreased as the nutrition level became low, could be explained in this manner. There were recognized high positive correlations between $\overline{RPGR}$ and $\overline{URA}$, so it was considered that the fact that $\overline{RPGR}$ decreased as time elapsed was brought about by the decline of $\overline{URA}$ with time. The differences of the plant growth by planting densities and nutrition levels could partly be explained in relation to root behavior by using the above mentioned method of the root growth analysis.

There were no remarkable differences of $\overline{URA}$'s value between A *sp.* and B *sp.* irrespective of changing plant densities and nutrition levels, except the result that $\overline{URA}$ value in high planting density in A *sp.* was larger than B *sp.* in early stage of growth. There was no difference of $\overline{RWR}$ between A *sp.* and B *sp.* in high nutrition level (NO_3-N:50 ppm). In low nutrition level (NO_3-N:10 ppm), however, there was the tendency that $\overline{RWR}$ in A *sp.* was larger than in B *sp.*.

It was considered that the direction of plant growth may shifted from the top to the root in the weeping type A *sp.* owing to the severe mutual interaction between leaves of tops in the weeping type plants compared with the plant growth of the erect type B *sp.*.

Total plant growth (top growth+root growth) was little influenced by the change of environmental factors on the middle way of the experimental period, although the interrelationships between top growth and root growth were liable to vary as the environmental factor changed[7].

As to the T/R 3-D ratio[6,7] which indicates the spatial relationship between top and root, there was the tendency that the value in B *sp.* was larger than in A *sp.*. T/R 3-D ratio, the ratio of the relative space density, in weep type plant was smaller than in erect type plant.

It was suggested that the direction of plant growth should be varied through the medium of the relative space density between top and root with the difference of plant type.

It was considered that this was one of the differences in the appearence of competition by plant types. There was no remarkable differences in $\overline{RAR}$'s value between plant types, although significant difference between A *sp.* and B *sp.* in low planting density (9 cm×9 cm) and high nutrition level (NO_3-N:50 ppm) were recognized in later stage of growth.

Summary

The plant growth analysis had been developed mainly, so far, based on the leaf area as a assimilative structure which concerned with photosynthetic capacity of plants.

Total plant dry weight should be comprehended as the sum of top dry weight and root dry weight, so that the root system and its physiological activity, through which

water and various minerals were absorbed and translocated must be inevitably taken into account for the plant growth analysis.

We tried to discuss the plant growth through the mediation of the top-root relationships and physiological activity of root. In the present paper, we introduced a new idea of "root growth analysis" to take the relative amount and activity of root into the concept of plant growth analysis, and pointed out that relative plant growth rate (RPGR) could be expressed by the product of 3 terms i.e. unit root activity (URA), root weight ratio (RWR) and root assimilation rate (RAR). The results obtained were as follows;

1. As an aid to deal with the relative total plant growth rate (RPGR) in relation to the root behavior and activity, the following equation was introduced,

$$\frac{1}{Pw}\cdot\frac{dPw}{dt}=\frac{\text{Root activity}}{Rw}\times\frac{Rw}{Pw}\times\frac{1}{\text{Root activity}}\cdot\frac{dPw}{dt}$$

$$(RPGR)=(URA)\times(RWR)\times(RAR)$$

In this way, relative plant growth rate (RPGR) can be divided into 3 terms which involves both root activity and top-root relationship.

2. (Total α-NA oxidizing activity in roots/hr)/(root dry weight) was named unit root activity (abbreviated as URA). URA decreased as time elapsed irrespective of the treatments as far as the experiment concerned, and there was no remarkable difference of $\overline{URA}$ between nutrition levels, significant difference was, however, recognized between planting densities.

3. RWR, ratio of root dry weight to the total plant dry weight (abbreviated as RWR), indicates the distribution ratio of dry matter produced by photosynthetic organs of plant between roots and tops. There was little difference of $\overline{RWR}$ between planting densities in high nutrition level, but a considerable difference was shown between planting densities in low nutrition level. Seeing from the nutrition levels, $\overline{RWR}$ became larger as nutrition level lowered irrespective of the planting densities.

4. Increasing rate of total plant dry weight per unit α-NA oxidizing activity in roots was called root assimilation rate (abbreviated as RAR). The tendency of decrease of $\overline{RAR}$ value according with the increase of planting density was shown, as D(9)>D(6)>D(3), and the difference of RAR's value between planting densities increased as time elapsed.

5. The relative growth rate of total plant dry weight (RPGR) was expressed by the mathematical terms of $1/Pw\cdot dPw/dt$ RPGR decreased as time elapsed and there was the tendency that large RPGR value was shown in low planting density, as D(9)>D(6)>D(3), and was the tendency that RPGR in low nutrition level (NO_3-N: 10 ppm) was smaller than those in high nutrition level (NO_3-N:50 ppm).

6. As to the difference in the appearance of competition between plant types, A *sp.* and B *sp.*, there was the tendency that RWR in A *sp.* was larger than in B *sp.* in low nutrition level (NO_3-N:10 ppm), but differences in $\overline{URA}$, $\overline{RAR}$, and $\overline{RPGR}$ were not recognized between plant types.

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〔和 文 摘 要〕

作物の個体間競合に関する研究

第4報 地下部から見た個体の生長解析法

鯨 幸 夫・神 田 巳季男

（東北大学農学研究所）

生長解析法は，作物の生長を光合成組織としての葉面積を基盤として，定量化するところから始った．しかるに，個体の生育量は，地上部生育と地下部生育との和として示され，かつ，生長の源となる養・水分が，根の生理活性や，地上部—地下部の相互関連性を，媒介として吸収され，地上部へと移動することを考慮した場合，地上部—地下部の相互関連性と，地下部の生理活性を定量化した上で，個体の生育を論じる必要性が生じてくる．そこで，筆者らは，上記の考え方に基づいて，個体の相対生長率 (RPGR) を，根の生理活性の程度 (URA) と，乾物の分配率 (RWR)，それに，根の生理活性の強さに対する個体の生長率の程度 (RAR) という，3つの要素の積として表示する可能性を示唆した．結果の概要は以下の通りである．

1. 地下部の生理活性（根の α-ナフチルアミン酸化力）や地上部—地下部の相互連関性を定量化した形での個体の生長解析法を検討すると，以下の関係式が成立する．

$$\frac{1}{Pw}\cdot\frac{dPw}{dt}=\frac{\text{Root Activity}}{Rw}\times\frac{Rw}{Pw}\times\frac{1}{\text{Root Activity}}\cdot\frac{dPw}{dt}$$

$$(RPGR)=(URA)\times(RWR)\times(RAR)$$

（ここで，Pw は個体乾重，Rw は地下部乾重，Root Activity は単位時間当の α-NA 酸化量を示す.）

従って，個体の相対生長率は，上記の3つの要素の積として示され，作物群内での個体の生長を，地下部の生理活性と，地上部—地下部の相互関係から検討できることが示された．

2. （個体の全 α-NA 酸化量/hr)/(根乾重）を，Unit Root Activity (URA と略記）と呼ぶ．URA の培地養分レベル間での差異はほとんど認められなかったが，栽植密度間での差異は顕著であった．

3. 個体全乾重に対する地下部乾重の割合を，Root Weight Ratio といい，RWR で表示すると，これは生産された乾物の分配率を示すことになる．RWR の栽植密度間差異は，高 NO_3-N 培地 (50 ppm) では，認められなかったが，低 NO_3-N 培地 (10 ppm) では，認められ，培地養分濃度が低下すると，いずれの栽植密度においても，RWR は増加を示した．

4. 根の生理活性の強さ (α-NA 酸化量の程度) に対する，個体の乾物増加率の比を，Root Assimilation Rate (RAR) と呼ぶ．RAR は，栽植密度が小さいほど大となる傾向を示し，生育が進むにつれ，栽植密度間で，RAR 値は，大きくなる傾向を示した．

5. 個体の乾物増加率は，$\frac{1}{Pw}\cdot\frac{dPw}{dt}$ で示され，RPGR は生育が進むにつれ，減少する傾向が認められた。RPGR は，栽植密度が小さいほど大となる傾向を示し，また，養分濃度（培地 NO_3-N レベル）を低下させると，RPGR の値も減少する傾向を示した。

6. 草型の違いによる，競合機構の違いを，Root Growth Analysis の方法で検討してみると，低濃度培地で，A sp. (Weeping type) の RWR が，B sp. (Erect type) より大きい傾向が認められたが，他の要素に関しては，草型による顕著な差は，認められなかった．