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BOTANICAL BRIEFING

Dynamics of Leaf and Root Growth: Endogenous Control versus Environmental Impact

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• *Aims* Production of biomass and yield in natural and agronomic conditions depend on the endogenous growth capacity of plants and on the environmental conditions constraining it. Sink growth drives the competition for carbon, nutrients and water within the plant, and determines the structure of leaves and roots that supply resources to the plant later on. For their outstanding importance, analyses of internal growth mechanisms and of environmental impact on plant growth are long-standing topics in plant sciences.
• *Scope* Recent technological developments have made it feasible to study the dynamics of plant growth in temporal and spatial scales that are relevant to link macroscopic growth with molecular control. These developments provided first insights into the truly dynamic interaction between environment and endogenous control of plant growth.
• *Conclusions* Evidence is presented in this paper that the relative importance of endogenous control versus the impact of the dynamics of the environment depends on the frequency pattern of the environmental conditions to which the tissue is exposed. It can further be speculated that this is not only relevant within individual plants (hence leaves versus roots), but also crucial for the adaptation of plant species to the various dynamics of their environments. The following are discussed: mechanisms linking growth and concentrations of primary metabolites, and differences and homologies between spatial and temporal patterns of root and leaf growth with metabolite patterns.

Key words: *Nicotiana tabacum*, leaf growth, root growth, image processing, endogenous control, dynamics of environment.

PLANT GROWTH IN A PERMANENTLY CHANGING ENVIRONMENT

Higher plants are sessile life forms and thus have to cope with varying environmental conditions in all their tissues and organs at all times of their life cycle. Some life forms escape from adverse conditions by, for example, limiting their activity to periods with little stress—by developing durable forms such as seeds, bulbs or rhizomes during what are likely to prove stressful periods in their life (Raunkiaer, 1934). However, such adaptations are only suitable to stressful situations that are at least to some degree predictable (e.g. through day length) or that develop slowly enough to allow plants to respond with strong functional and structural changes. Less predictable or short-term fluctuations of environmental factors are usually coped with by acclimatization mechanisms within the physiological limits of individual plants (Lambers *et al*., 1998).

However, plants do only need to respond to environmental changes if these changes really affect plant performance. Short-term changes in, for example, temperature or light conditions over the range of minutes will probably not be relevant, as the plant integrates over such fluctuations (Granier *et al*., 2002). However, if heterogeneous environmental conditions alter the availability of resources in time and space, plants have to respond adequately to optimize their resource acquisition. Such situations are given, for example, for roots exposed to uneven distribution of nutrients in the soil (Göttlein and Stanjek, 1997). The dynamics of environmental conditions must be linked to the sensitivity of plant response and thus to endogenous control systems.

ENDOGENOUS CONTROL OF PLANT GROWTH AND METHODS TO MAP GROWTH IN SPACE AND TIME

In contrast to higher animals, plants are built from a successive arrangement of modules that enables them to grow during their entire lifetime (Scanlon, 1998; Walter and Schurr, 1999). This modular pattern is the basis of plant adaptation to changing environments (Schulze, 1982). The general growth pattern of plant organs is genetically fixed (Poethig and Sussex, 1985), but can be strongly modified by environmental conditions. Studying the dynamics of the distribution of area expansion in broad-leaved species (dicots) was hitherto hampered by the absence of suitable methods (Avery, 1933; Maksymowych, 1973; Schurr, 1997). In monocotyledonous species, leaf growth dynamics have been followed for decades by use of linear variable displacement transducers that are attached to the leaf tip and measure the velocity of leaf elongation (since expansion processes occur in basal leaf parts that are completely enclosed in sheaths of older leaves, it is not possible to use optical methods). For all species investigated, clear diurnal rhythms have been observed (see references in Table 1). However, such results were often based on only a small number of replicates; temporal resolution

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TABLE 1. *Diurnal variation of leaf growth rate in monocotyledonous and dicotyledonous plants*

Species	Maximum relative growth rate				Method	Author
	Day	Dusk	Night	Dawn		
Monocotyledons						
Zea	X				LVDT	Watts (1974)
	X				Ruler	Acevedo *et al*. (1979)
Triticum	X				LVDT	Christ (1978)
Sorghum	X				Ruler	Acevedo *et al*. (1979)
Festuca			X		LVDT	Durand *et al*. (1995)
Oryza	X				LVDT	Seneweera *et al*. (1995)
Dicotyledons						
Helianthus			X		Ruler	Boyer (1968)
Glycine			X		Ruler	Bunce (1977)
Phaseolus	X				LVDT	Davies and van Volkenburgh (1983)
Vitis	X				LVDT	Shackel *et al*. (1987)
Ricinus				X	DISP	Schmundt *et al*. (1998)
Nicotiana				X	DISP	Walter and Schurr (2000)
Populus		X			DISP	Walter *et al*. (unpubl. res.)

LVDT, Linear variable displacement transducer; DISP, digital image sequence processing.

was relatively low and spatial resolution completely lacking. Spatial variation was analysed by the pinpricking method (Kemp, 1980; Fricke *et al*., 1997), in which a pattern of holes is produced in the expansion zone of leaves, located within the intact sheath of the next leaves, by thin needles. The change in distance between those holes after some time is used to calculate growth distributions. Although the resolution of this method is limited, these studies led to important hypotheses on the basis of diurnal variation in monocotyledonous leaf growth, like control by sucrose phosphate synthase activity and carbohydrate metabolism (Seneweera *et al*., 1995), control by shoot apical meristem temperature or by turgor (Watts, 1974).

To link macroscopic growth with the underlying control processes of gene expression, cell division and expansion as well as differentiation, growth needs to be studied in temporal and spatial scales of hours to minutes and milli- to micrometers, respectively. Molecular control processes of cell division (e.g. Beemster *et al*., 2003) and cell expansion (e.g. Vissenberg *et al*., 2000; Cosgrove *et al*., 2002) have been studied intensively in recent years. However, the interaction of these internal processes with the dynamics of external conditions is still scarcely known. Recent results suggest oscillations of cytoplasmic free calcium play an important role at second messenger level, linking external parameters like day length with endogenous signalling pathways (Love *et al*., 2004).

Only recently have methods to analyse growth of dicotyledonous leaves with relevant spatial and temporal precision been implemented (Schmundt *et al*., 1998; Walter *et al*., 2002*a*, *b*; van der Weele *et al*., 2003). Digital image sequence processing approaches (Bigün and Granlund, 1987; Haußecker and Spies, 1999) have been applied to time-lapse-videos of growing leaves and roots (Figs 1 and 2). These methods work in a similar manner to the human motion perceptive system (Schrater *et al*., 2001) and are applicable to processes of very different geometries and scales. They are not only more precise than traditional ones, but also less invasive, highly automated and applicable on both above- and below-ground plant organs.

IMPACT OF ENVIRONMENT ON GROWING TISSUES

The impact of environmental constraints on growth can either be direct, via physical conditions on primary growth processes, or indirect, due to developmental adaptation. Numerous environmental factors affect plant growth (Marschner, 1995; Lambers *et al*., 1998). Water shortage and excess, temperature, nutrients and light are just a few examples of abiotic factors interacting with growth directly or indirectly. Biotic interactions can also either affect growth directly (e.g. herbivory) or indirectly via changing resource availability. Negative effects on plant growth are, for example, produced by competition; positive effects are often generated in symbiotic associations such as in mycorrhizal systems in which the fungal partner provides additional phosphate for the plant partner in poor soils. The strength by which environmental conditions affect growth depends on their dynamic behaviour. Strongest growth effects are found when the environmental parameters change very abruptly and induce acute stress conditions such as rapid drought or heat stress. Smoothly changing environmental constraints can lead to acclimatization processes within plants that adjust their performance to the environmental conditions. In the best case (for the plant), this causes non-stressful changes in plants, even when resources are limiting (Ingestad and Agren, 1992).

Most growth effects have been investigated extensively on a relatively coarse scale, relating environmental constraints to yield or to overall plant biomass (Marschner, 1995; Lambers *et al*., 1998). The following paragraphs review recent results on growth of leaves and roots as the two major competing sinks for carbon, nutrients and water in the vegetative state of herbaceous plants. *Nicotiana*

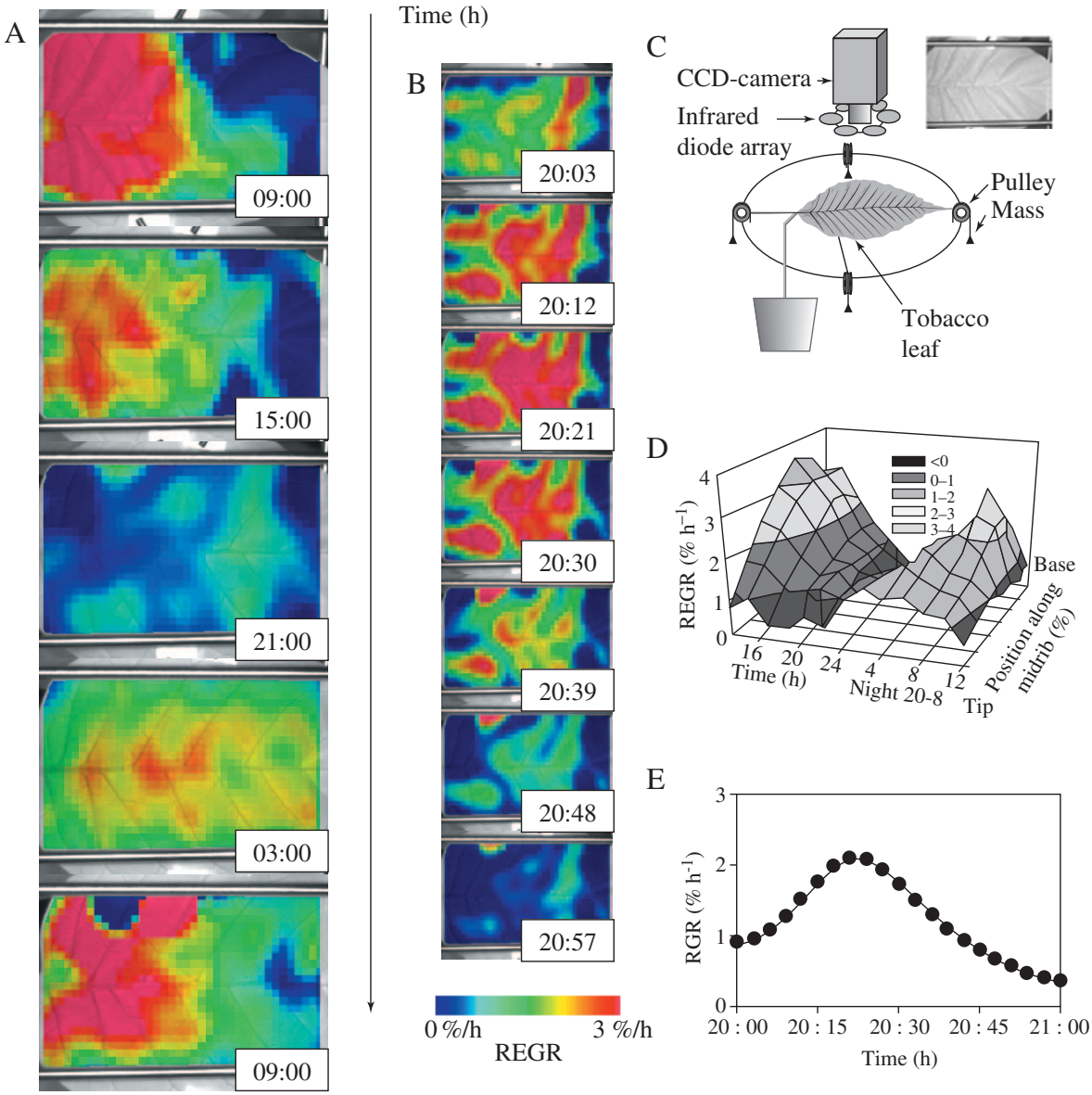
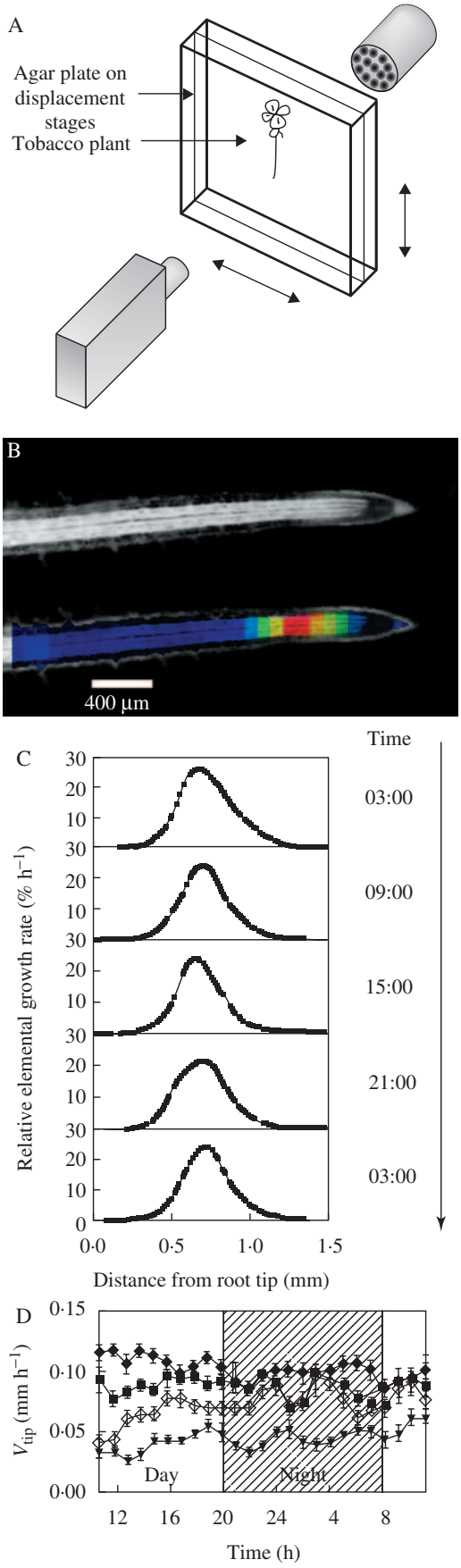


FIG. 1. Spatio-temporal patterns of leaf growth in *Nicotiana tabacum*. (A) Instantaneous, colour-coded distributions of relative elemental growth rates at five different times throughout the diurnal course (night 2000–0800 h). (B) Sequence of instantaneous, colour-coded distributions of relative elemental growth rates (REGR) in response to a day–night transition. (C) Set-up for leaf-growth monitoring and original image. (D) Spatio-temporal distribution of relative elemental growth rates along the midvein (averaged over 2 h and 15 % midvein length). (E) Average relative growth rate (RGR) of the leaf depicted in (B) during the first hour of the night.

tabacum is used as a model system for the detailed investigation of spatial and temporal patterns of growth processes linking them to endogenous and exogenous parameters. Strong differences in their internal growth characteristics and the control via the environment have been observed.

LEAF GROWTH: ORGANIZATION AND DYNAMICS

Leaves of dicotyledonous species produce a limited number of cells and, in a given environment, these cells expand deterministically until their final size is reached. During this process, cell division ceases after different times and in an environment-dependent pattern in epidermis and mesophyll tissues (Roggatz *et al*., 1998). In tobacco leaves, mean growth rates decline exponentially from leaf emergence to the fully grown state within about 2 weeks (Avery, 1933; Walter and Schurr, 1999). The primary temporal pattern to be found in growing leaves is a diurnal cycle with a maximum expansion growth rate of up to 6 % h^{-1} in tobacco (Fig. 1A and D). In this species the maximal growth activity generally occurs at the night–day transition; the minimum is found 12 h later at the day–night transition. This is in contrast to grasses, where the maximum growth rate was often found in the middle of the day (e.g. Seneweera



et al., 1995). Although phasing and amplitude of this diurnal cycle differs between species (Table 1), diurnal changes in expansion growth rate are generally significantly larger than the changes in mean expansion growth rate from day to day. This shows that the extent to which different specific mechanisms control the diurnal change of leaf growth must vary between species; but this shows also that control processes acting on growth variations within 24 h are stronger than leaf ageing processes acting on a day-to-day scale in all species investigated so far.

Circadian, oscillating growth activities in tobacco continue for up to 2 weeks after plants are transferred from 12 h light/12 h dark to a continuous light regime (M. M. Christ and A. Walter, unpubl. res.). Mechanistic explanations for the occurrence of the observed diurnal growth cycle do not exist so far. Biophysically, growth is regulated by the interaction between internal plant pressure (turgor) as the driving force and the rigidity (or extensibility) of the cell wall as the retarding force (Lockhart, 1965; Cosgrove, 1986). In the context of growth control within a circadian framework, the controlling mechanisms have to alter biophysical properties such as turgor or cell wall rigidity in a circadian manner.

A base–tip gradient is the most prominent spatial pattern to be observed throughout the entire diurnal course of tobacco leaf growth (Fig. 1). Patches and irregularities of this gradient are present in short-term (minutes) growth measurements (Fig. 1A and B). Smooth gradients are found when values are averaged for time intervals of 1 h or more (Fig. 1D). Hence, small-scale changes in local expansion are very interesting in the context of growth control mechanisms; any irregularity in such a gradient would result in buckling of the leaf surface or must be compensated by adequate spatial and temporal growth processes in the leaf. Biomechanics might thus also provide an interesting alternative, or contributory factor, in controlling growth and shape in planar plant organs such as leaves—in a similar way as previously proposed for meristems (Green, 1992). External straining forces applied for technical reasons in the course of the measurement can affect those small-scale growth variations under special conditions, but do not interfere with the general base–tip gradient when an appropriate force is chosen (Walter *et al*., 2002*a*). The base–tip gradient develops in parallel to the maturation of cells that occurs first in the leaf tip and then proceeds to the leaf base (Avery, 1933).

Environmental conditions can alter the diurnal pattern of leaf expansion; while drought stress (Schurr *et al*., 2000), nutrient deficiency and various temperature regimes (A. Walter and L. Ainsworth, unpubl. res.) affect only the amplitude but neither the shape nor the phasing of

FIG. 2. Spatio-temporal patterns of root growth in *Nicotiana tabacum*. (A) Set-up for root growth monitoring. (B) Original image and colour-coded distribution of relative elemental growth rates. (C) Instantaneous distributions of relative elemental growth rates at five different times throughout the diurnal course (night 2000–0800 h). (D) Growth velocity of the root tip (V_{tip}) during four typical diurnal courses (1-h mean values and variations).

the cycle, increased atmospheric CO_2 concentrations have been shown to cause a transient growth reduction in the afternoon in growing cottonwood leaves (Walter *et al*., unpubl. res.).

Short-term variations of environmental conditions cause rapid, but transient changes in leaf expansion in all investigated species: When lights are switched off, a steep increase occurs with growth rates of up to 10 % h^{-1}, followed by an exponential decrease with a decay time of approx. 15 min (Fig. 1B and E). When lights are switched on, the opposite behaviour is observed in tobacco. Such transient growth spikes have also been observed in monocot leaves (Hsiao *et al*., 1970; Christ, 1978). In contrast to the diurnal growth activity, these transient growth spikes are brought about by a uniform variation throughout the entire leaf (Fig. 1). Step changes in light intensity do exert fast effects on, for example, cell wall pH (Mühling *et al*., 1995) and thus may affect cell wall extensibility. They also affect stomatal conductance (Mott and Buckley, 2000) and, most likely, leaf water potential and may thus influence turgor.

In summary, leaves follow an endogenous pattern of cell division and elongation and are only transiently affected by abrupt changes in the environment. Therefore leaf growth control seems to be well buffered from direct external impact. As external factors like temperature or light regimes fluctuate strongly, direct impact on leaf growth locally and immediately could adversely affect leaf growth processes and leaf shape. It can be hypothesized that the robust control mechanisms of leaves have evolved to create persisting growth patterns and leaf shapes in a fluctuating environment.

ROOT GROWTH: ORGANIZATION AND DYNAMICS

In contrast to leaves, roots form new cells permanently at the root tip and expand them in the proximal expansion zone. This leads to a permanent stream of new cells through the growth zone of root tips. Diurnal expansion patterns are not present in growing root tips (Fig. 2C and D). This has not only been shown for tobacco roots, but also for roots of many other species [e.g. cherry, rice, sorghum, and maize as observed by Head (1965), Iijima *et al*. (1998) and Walter *et al*. (2002*b*), respectively]. Secondary temporal fluctuations of root growth can be induced by repetitively changing environmental factors such as root zone temperature, to which root growth is highly susceptible (Walter *et al*., 2002*b*). However, the natural temperature regime to which roots are exposed is much more constant than the one to which a leaf is exposed. With the large heat capacity of wet soil, plants will only be exposed to significant changes in temperature if, for example, a heavy rainfall changes soil temperature. Thus roots might not require the same buffering mechanisms of growth as leaves. However, buffering from temperature changes above ground will not be as efficient in dry soil and roots will be exposed to much higher temperature variation in such environmental conditions.

The spatial distribution of relative elemental growth rate within the root growth zone is more complex than in the dicot leaf. Within the meristem, the expansion growth rate is relatively low since repetitive cell divisions take place at rates between one division per day and one per week (Silk, 1984). Cell division and re-growth of daughter cells to the initial mother cell size results in a biomass increase of a factor of two. This is the reason for expansion growth rates of <5 % h^{-1} in the meristematic region. In tobacco roots, expansion growth rate increases with the onset of gross cell elongation, soon reaching a maximum of 25 % h^{-1} at 0.7 mm behind the root tip (Fig. 2B and C). Behind the zone of maximal expansion growth activity, the relative elemental growth rate declines steadily as the cells develop to maturity. The basic shape of this growth rate distribution can be modelled *a priori*—using relatively simple assumptions—from the influx of two counteracting hormones entering the root growth zone from different directions (Chavarria-Krauser and Schurr, 2004).

In maize roots, often two transient maxima can be distinguished that alter their relative intensity with altering external nutrient availability (Walter *et al*., 2003). While in nutrient-free solution, the apical one is higher, full-strength nutrient solution leads to a more pronounced basal peak of the growth rate distribution. Growth rate distributions within the maize root growth zone can be altered by a variety of environmental situations (Pritchard, 1994), such as temperature fluctuation (see above, Pahlavanian and Silk, 1988; Walter *et al*., 2002*b*), water deficit (Fan and Neumann, 2004) or nutrients.

In conclusion, both leaf and root show adaptation to environmental conditions; while roots respond strongly and probably directly to changes in their environment, leaf growth-control mechanisms compensate for short-term changes in the environment. Therefore it is proposed that control mechanisms buffer leaf growth from rapid fluctuations, while, for root growth, control mechanisms need to respond immediately to environmental parameters like nutrient concentration to optimize attributes such as nutrient use efficiency in soils with patchy nutrient availability.

GROWTH OF ISOLATED PLANT TISSUE: TISSUE CONTROL PROCESSES ARE THE BASIS OF SENSITIVITY TO ENVIRONMENTAL PARAMETERS

The diurnal change of growth-rate gradients contrasts strongly between roots and leaves. These differences in growth behaviour might be linked to the different duration of the cell elongation process; cellular development proceeds at different velocities in root and leaf, respectively. While in roots, the elongation of an individual cell is finished within several hours, cells of dicot leaves typically take 2 weeks to expand to maturity. Since organ-specific spatial growth-rate gradients follow the cellular developmental gradients within growth zones, it is important to investigate the growth behaviour of smaller, isolated tissue systems between the level of cells and tissues.

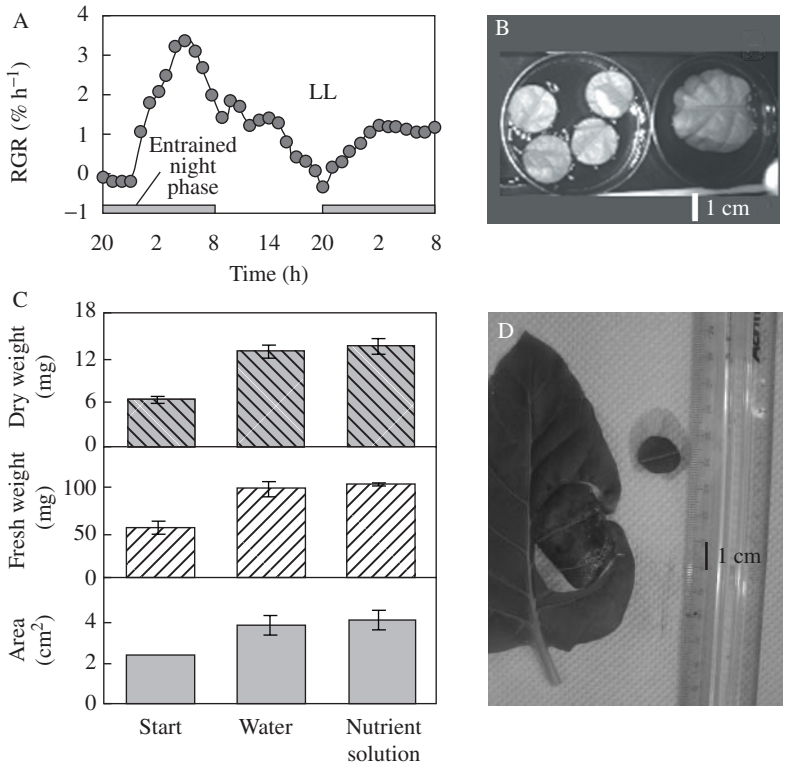


FIG. 3. Growth of isolated leaf discs, cut from growing leaves of *Nicotiana tabacum*. (A) Relative growth rate (RGR) of a leaf disc floating on nutrient solution in continuous light (LL), 24 h after cutting the disc from a plant that was adapted to 12 h/12 h light/dark (entrained night phase shown in panel). (B) Visualization of leaf disc growth within 4 d. Discs in left Petri dish were cut immediately prior to taking the picture, while disc in the right Petri dish was cut with the same cork borer 4 d earlier. (C) Growth of leaf discs ($n = 6$, mean value and standard error) in area, fresh and dry weight 5 d after incubation (12 h/12 h light/dark). The leaf discs were all cut with the same borer (17.5-mm diameter) and were incubated either on nutrient solution or double-distilled water. (D) Growth of a leaf disc and of the leaf from which the disc was cut initially. Four days after cutting, the leaf disc, which had floated on nutrient solution, was put back in the hole of the leaf. The leaf was attached to the intact plant for the entire time. The small leaf disc to the right is cut from another leaf and depicts the size of the incubated leaf disc at the time of cutting. Due to the convex shape of the incubated leaf disc, disc and hole do not match perfectly.

Isolated leaf discs and cylindrical root segments from growing organs were used to investigate control mechanisms of growth. In leaf discs with diameters between 4 and 20 mm that were punched from growing tobacco leaves and then floated on nutrient solution, diurnal rhythmicity of growth was present in the same frequency and amplitude as in the intact leaf (Fig. 3). In continuous light, circadian growth rhythms were detectable for up to 2 weeks. In light/dark conditions, the short-term growth rate oscillations after stepwise light changes were also present. Therefore, it can be concluded that the diurnal growth rhythm of the leaf does not depend on the supply of hormones or other factors from other parts of the plant, but is an intrinsic property of the leaf tissue, which is controlled by an intrinsic clock.

Isolated root segments showed a completely different behaviour; neither incubation in water or nutrient solution nor addition of sucrose to the incubation medium resulted in sustained growth of excised elements of the root growth zone. This is strong evidence that permanent influx of hormones or other signalling substances from the rest of the plant is absolutely crucial for root growth. Supplementations of hormones can, for example, promote growth of rootlets in tissue culture.

This strong difference in the organization of growth control in roots and leaves may provide the basis for the difference of these tissues in sensitivity to environmental constraints.

DO METABOLITES MEDIATE ENVIRONMENTAL CHANGES AND ENDOGENOUS GROWTH CONTROL?

The correlation between growth patterns and metabolite concentrations might give a hint into the biochemical cause for such differences between root and leaf growth control in variable environments. In a large number of experiments, concentrations of carbohydrates, amino acids, organic acids and ions in growing and mature leaves of tobacco and castor bean, as well as in growing maize roots were analysed (for methods and spectrum of compounds refer to Walter *et al.*, 2002*a*, 2003). In growing tobacco leaves, the concentrations of several metabolites showed pronounced diurnal variations (Fig. 4A), while in fully grown leaves such changes were absent. Sucrose and glutamine, which are essential substrates for biosynthesis of primary metabolites, reached peak values around dusk—thus at a time when leaf growth is at its minimum. This

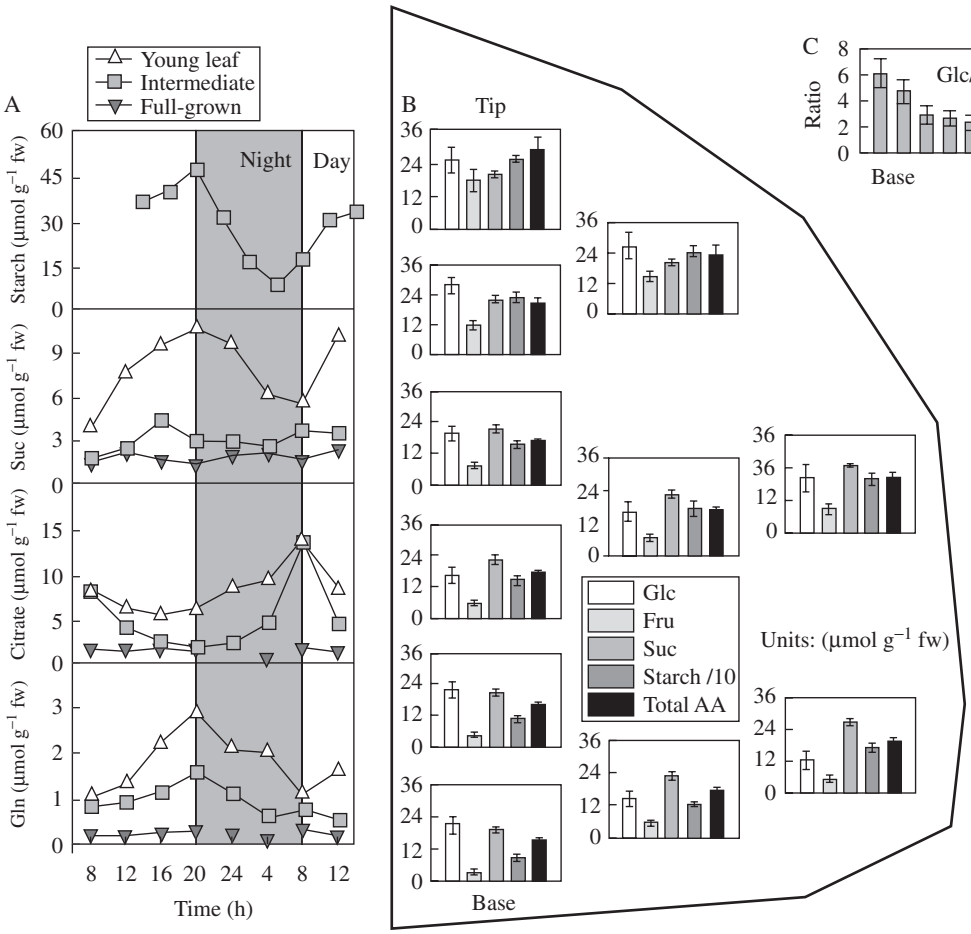


FIG. 4. Metabolite concentrations in growing and mature leaves of *Nicotiana tabacum*. (A) Time series of starch, sucrose (Suc), citrate and glutamine (Gln) in young, intermediate and full-grown leaves of *Nicotiana tabacum* throughout the diurnal course. For Suc, citrate and Gln, three leaves of different positions within the same plant were chosen for taking the samples of each point in time. For the young and full-grown leaf, two leaf discs were pooled for the sample. For the intermediate leaf, mean value and standard error of four separately analysed samples are depicted. The eight plants used for this experiment were taken from a total population of 24 plants and were selected for comparable growth rates of the three leaf developmental states investigated: intermediate leaves (RGR = 45 ± 5 % d^{-1}); young leaves, three positions above (RGR = 90 ± 10 % d^{-1}; full-grown leaves, three positions below intermediate leaves (RGR = 0 % d^{-1}). For starch, the samples were taken from intermediate leaves of another population of plants. (B) Spatial distribution of glucose (Glc), fructose (Fru), sucrose (Suc), starch and total amino acids (Tot AA) throughout the leaf blade in inter-veinal tissue of intermediate leaves of *Nicotiana tabacum*. Samples were taken at the indicated positions along the leaf developmental axes in parallel to the midvein and the side veins of first order ($n = 6$, mean value and standard error). The six plants used for this experiment were taken from a total population of 24 plants and were selected for comparable growth rates of intermediate leaves (RGR = 45 ± 2 % d^{-1}). (C) Ratio of glucose/fructose (Glc/Fru) along the leaf midvein, calculated from the values depicted in (B) (mean values and standard error).

excess of growth substrates might at least be favourable if not necessary for the re-initiation of growth processes that use these substrates for synthesis of structural macromolecules as cellulose or various proteins. This mechanism would explain the observed phase shift of the diurnal rhythms of substrate concentrations and growth rates. The role of citrate would be to compensate the loss of negatively charged sugars and amino acids during their prime times of metabolism and thus to provide charge balance within the cell at every point in time.

The diurnal metabolism of carbohydrates affects diurnal growth patterns in transgenic potato plants (Kehr *et al*., 1998), the metabolism of starch is regulated diurnally (Geiger *et al*., 2000), and the concentrations of starch and sucrose (Matt *et al*., 1998) as well as hexoses (Kemp and Blacklow, 1980; Chia *et al*., 2004) change diurnally due to the temporal course of photosynthesis. It has now been shown that the concentrations of several compounds exert pronounced diurnal variations in young developing leaves with a phase shift in relation to the diurnal growth variation. The observed antiparallel behaviour of sugars and glutamine relative to expansion growth favours the view that an excess of growth substrates is necessary for the re-initiation of growth processes during the diurnal cycle. A temporally constant amount of anions might be sustained via the diurnally fluctuating concentration of citrate, which presents a flexible means of fast charge balance in growing tissues (Martinoia and Rentsch, 1994).

A possible connection between the carbohydrate pool of a growing leaf and the extensibility of the cell wall was indicated recently by experiments showing, that pronounced internal strain forces and energy supplied from starch breakdown may be a requirement for regular growth patterns (Walter *et al*., 2002*a*).

Spatial patterns of leaf growth cannot be easily linked to local metabolite concentrations. Almost all studied metabolites were more homogeneously distributed than growth rates (Fig. 4B). There is almost no literature with which this data can be directly compared, but enzyme activity studies of sucrose synthase and sucrose phosphate synthase (Schurr *et al*., 2000) do also indicate quite homogeneous distributions of metabolites within the leaf blade of growing leaves. The most consistent correlation between the spatial distribution of growth rates and metabolite concentrations was found for the ratio between glucose and fructose concentration, which declines from leaf base to tip in a similar manner to the fall in growth rate (Fig. 4C). This favours the view that high Glc-levels are necessary in actively growing tissue. Measurements of involved enzymes such as hexokinases and phospho-gluco-isomerases have to be performed in future studies to test this hypothesis.

In growing roots, the analysed metabolites show constant concentrations throughout day and night (Walter *et al*., 2003). This common relationship between concentrations of primary metabolites and growth activity suggests a common mechanism between growth dynamics and compound concentrations in roots and leaves.

As expected from the hypothesis, the spatial distribution of different compounds does also strongly differ between roots and leaves. While growing leaves show only weak gradients of compound concentrations from base to tip (Fig. 4B), strong differences are found between base and tip of the root growth zone (Walter *et al*., 2003). Computation of deposition rates for those compounds in different segments of the growing root shows, that the deposition rate profiles of most substances resemble the shape of the distribution of the relative elemental growth rate along the root growth zone (Silk, 1984; Walter *et al*., 2003). Several ions have maximal deposition rates apical of the maximum relative elemental growth rate, while sugars show a maximal deposition rate slightly behind the maximum of the growth rate distribution. While ions can only be stored in an osmotically active form, carbohydrates can be polymerized and thus be osmotically inactivated. This may cause significant differences in the response of root growth distribution in response to excessive carbohydrates versus nutrients.

Obviously, the interaction between environmental and endogenous control of growth is a complex network. The few results concerning metabolite concentrations mentioned here show that growth patterns are indeed correlated to, and hence most probably regulated by, physiological processes that act within hours to minutes and within spatial dimensions of tissues. Yet, those results also show that we have only started to understand some knots in the network of growth regulation; for a comprehensive view of this topic a lot of studies focusing on other regulatory levels of plant organization ranging from tissue biomechanics to gene expression have to follow.

CONCLUSIONS

The environmental conditions, to which leaf and root are exposed, might be the evolutionary reason for significantly different control mechanisms active at the two major sinks of the plant: leaves experience strong variations of external factors during 24 h and thus evolved a circadian growth behaviour, while roots with their steady growth behaviour are adapted to nearly constant external conditions. Hence, changes of environmental factors cause less direct effect in growing leaves compared with the root. This supports the hypothesis that the relative importance of endogenous control versus the impact of the dynamics of the environment of the growing organ must be balanced to obtain adequate plant behaviour in environments fluctuating at different frequencies. While leaf growth adapts to environmental conditions via leaf development, roots need to respond much quicker in order to optimize resource use efficiency.

The internal regulation of the growth processes has to be elucidated in future studies. A wide spectrum of mechanisms ranging from the molecular to the biophysical level has to be taken into account. The temporal and spatial scales that are relevant to link macroscopic growth with molecular control require the use of non-destructive, high resolution growth measurement methods. Recent investigations of molecular growth control using micro-array techniques (e.g. Horvath *et al*., 2003) and single-cell sampling (e.g. Roy *et al*., 2003) are important to elucidate how plants control growth processes on a molecular and cellular level. They have to be put into the context of tissue and whole-plant growth behaviour and might be able to solve questions like: In which way is carbohydrate metabolism involved in controlling diel growth dynamics? Are diurnal changes of turgor and leaf growth correlated with each other? What are the pathways relating environmental growth control with endogenous, circadian growth control? Are the different effects of environmental changes on leaf and root growth dynamics indicators for differential adaptation of tissue growth mechanisms to fluctuation frequencies of environmental factors to which tissues are exposed in nature?

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