Multi-scale phenotyping of leaf expansion in response to environmental changes: the whole is more than the sum of parts

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ABSTRACT

The leaf is a multi-scale dynamic unit that is determined by mechanisms at different organizational scales (cell, tissue, whole leaf and whole plant) and affected by both internal (genotype) and external (environmental) determinisms. The recent development of phenotyping platforms and imaging techniques provides new insights into the temporal and spatial patterns of leaf growth as affected by those determinisms. Conclusions about the overriding mechanisms often depend on the considered organizational scale and of time resolution which varies from minutes to several weeks. Analyses of leaf growth responses to environmental conditions have revealed robust emerging properties at whole plant or whole leaf scales. They have highlighted that the control of individual leaf expansion is more complex than merely the sum of cellular processes, and the control at the whole plant level is more complex than the sum of individual leaf expansions. However, in many cases, the integrated leaf-growth variable can be simplified to a limited set of underlying variables to be measured for comparative analyses of leaf growth or modelling purposes.

Key-words: abiotic stresses; Arabidopsis; leaf growth; maize; monocotyledons; multi-scale; phenotyping; sunflower.

INTRODUCTION

When exposed to challenging environmental conditions, plants increase or decrease leaf area via a combination of mechanisms which are controlled at different levels of organization. An environmentally induced change at a lower level of organization may or may not result in a change in final plant leaf area. For instance, both cell number and cell area are affected by environmental cues (Durand et al. 1995; Taylor et al. 2003; Kavanová et al. 2006; Kavanová, Lattanzi & Schnyder 2008), but the interplay between these two traits may result in a final leaf area that is unchanged (Hemerly et al. 1995; Horiguchi et al. 2006; Cookson, Chenu & Granier 2007; Ferjani et al. 2007), in a change in leaf area linked to cell number (Chiera, Thomas & Rufty 2002; Rymen et al. 2007) or a change in leaf area linked to cell size (Radin & Eidenbock 1984; Lecoeur et al. 1995). In the same way, changes in individual leaf area may or may not affect whole plant leaf area, depending on the relative changes in leaf area and leaf number (Wery 2005; Aguirrezabal et al. 2006). As a consequence, many mechanisms have been associated with the control of leaf growth including, e.g. cell cycle regulation (Beemster, Fiorani & Inzé 2003), tissue extensibility (Pien et al. 2001), hydraulic (Bouchabké, Tardieu & Simonneau 2006) and sugar signalling (Gibson 2005).

The genetic variability in leaf growth has been linked to processes at the different organizational scales. For example, quantitative trait loci (QTLs) of leaf area or biomass have been shown to co-localize with QTLs of variables as diverse as flowering time or leaf number (El-Lithy et al. 2004), leaf elongation rate (Reymond, Muller & Tardieu 2004; Ter Steege et al. 2005), duration of leaf elongation (Ter Steege et al. 2005), epidermal cell number and/or area (Rae et al. 2006; Zhang et al. 2007; Tisné et al. 2008), leaf shape (Rae et al. 2006) or plant relative growth rate (Ter Steege et al. 2005). Each of these processes may have an effect on final leaf area or biomass which can be substantial in some conditions and negligible in others, depending on the developmental pattern of the species or genotype in consideration, and also on the time course and intensity of the environmental cues. A few candidate genes and metabolites have been proposed to be involved in the response of leaf growth to environmental cues, but studies combining transcript analyses and appropriate leaf growth analyses are rare (Schümann et al. 1997; Ainsworth et al. 2006; Meyer, Steinfath & Liscic 2007; Muller et al. 2007). One reason for this is the difficulty to combine both types of analysis at appropriate and comparable spatial and temporal resolutions. Recently, phenotyping platforms have been developed to assess leaf growth at high throughput in different environmental conditions, thereby drastically increasing the number of studied genotypes, environmental scenarios and leaf growth variables (Granier, Aguirrezabal & Chenu 2006; Sadok et al. 2007; Walter et al. 2007; Weight & Parnham 2008). Depending on their throughput and on
their spatial and temporal resolutions, they make possible statistical and genetic analyses of leaf expansion, quantitative genetics of processes involved in leaf growth, or combined transcript and leaf growth analyses.

In this review, we discuss studies which dissect the effect of environmental stresses on leaf growth at different temporal and spatial scales as well as tools for crossing levels of organization. Even if in some cases responses at one scale can be inferred from responses at an underlying scale, they are generally more complex. A multi-scale phenotyping approach is often – but not always – required to highlight properties controlling changes in leaf growth when plants are grown in different environmental conditions.

**TEMPORAL AND SPATIAL PATTERNS OF ELONGATION IN MONOCOTYLEDONOUS LEAVES SUBJECTED TO ENVIRONMENTAL STRESSES**

Leaf elongation in monocotyledonous follows four developmental phases (Fig. 1a, Gallagher 1979 in wheat and barley; Skinner & Nelson 1995 and Durand, Schäufele & Gastal 1999 in tall fescue; Muller, Reymond & Tardieu 2001 in maize).

During the first phase, leaf length increases exponentially with time (Fig. 1a, inset; Gallagher 1979; Skinner & Nelson 1995), with a nearly constant cell length from the base to the tip of the young lamina. This suggests that both cell division and relative tissue elongation have the same rates, thus cell length remains constant and unaffected by growth (DEZ, Fig. 1b, in maize leaves smaller than 2.5 or 4 mm long in Durand et al. 1999 and Muller et al. 2001, respectively).

During the second phase, the absolute leaf elongation rate accelerates abruptly (Fig. 1a, Muller et al. 2001; Fournier et al. 2005). The growing zone progressively gets longer with time (GZ, Fig. 1b). It includes the cell-division zone (DEZ, Fig. 1b) and the elongation-only zone formed of cells increasing rapidly in size without cell division (EZ, Fig. 1b).

Those two first phases occur although the leaf is hidden by older leaves, from its initiation to its emergence. Effects of environmental conditions during those early phases have rarely been analysed because of technological difficulties, but also because of evidence for limited effects of environmental changes on final leaf area and maximal leaf elongation rate during this phase. For example, a reduction in incident light that is imposed during the first two phases causes a decrease in relative leaf elongation rate with no after-effect, neither on maximal absolute leaf elongation rate nor on final leaf length (Muller et al. 2001).

The third developmental phase is characterized by a constant absolute leaf elongation rate (‘linear phase’, Gallagher 1979; Skinner & Nelson 1995; Muller et al. 2001). During this phase, the spatial distributions of cell division and tissue expansion in the growing zone are time-invariant (steady state). The growing zone (GZ, Fig. 1b) has a constant length of 3–4 cm in tall fescue and in short Poa species (Durand et al. 1999; Fiorani et al. 2000) and 7–8 cm in maize (Tardieu et al. 2000). Cells continuously progress through this growing zone, from the basal meristematic region to distal, mature zones of the leaf. It takes the cells 1–2 d to cross the whole growing zone, i.e. to undergo the whole process of cell division and expansion (MacAdam, Volenc & Nelson 1989; Ben Haj Salah & Tardieu 1995). After crossing this zone, cells contribute to the mature zone which increases in size with time (MZ, Fig. 1b). Changes in temperature, evaporative demand and soil water content cause immediate changes in leaf elongation rate during this phase and recovery is rapid after the end of the stress (Durand et al. 1999; Sadok et al. 2007), suggesting that monocotyledonous leaves have a very short ‘memory’ regarding the elongation rate responses to environmental conditions. In most situations, the final leaf size and leaf elongation rate are reduced via a reduction in relative expansion rate in different parts of the growing zone and a reduction in the length of this zone as shown for low temperature (Rymen et al. 2007), water deficit (Tardieu et al. 2000), low nitrogen availability (Gastal & Nelson 1994), phosphorus deficiency (Kavanová et al. 2006) or salt stress (Bernstein, Silk &
Läuchli 1993). Changes in plant carbon status induced by changes in [CO₂] have a more controversial effect. An increase in carbon availability because of high [CO₂] has no effect on leaf area in wheat in some studies, although profound effects on whole leaf-growth kinetics have been observed in others (Masle 2000).

During the fourth developmental phase, both relative and absolute leaf elongation rate declined until the end of leaf elongation (Muller et al. 2001; Fournier et al. 2005). This coincides with a decrease in cell production at the base of the leaf, suggested to cause a later decline in cell wall plasticity and cell elongation rate (Palmer & Davies 1996; Fournier et al. 2005). Even though examples in the literature are rare, the last phase of leaf elongation can be affected by environmental stresses, thereby affecting the duration of elongation and final leaf area. For example, the increase in leaf length of tall fescue plants grown in low blue light is accompanied by an increase in the duration of leaf elongation (Gautier & Varlet-Grancher 1996), and the decrease in leaf length in maize plants grown under low nitrogen conditions is accompanied by an increase in the duration of leaf elongation (Jovanovic et al. 2004).

Leaf expansion and its alteration by environmental changes in monocotyledonous leaves is thus characterized by (1) a long ‘linear’ phase of elongation with both constant absolute leaf expansion rate and a fixed growing zone; (2) a very rapid effect of environmental changes both on spatial and temporal patterns of elongation during this linear phase; and (3) no clear after-effects of environmental changes on absolute leaf expansion rate. Leaf elongation rate is more plastic than the duration of elongation and is remarkably correlated to the final leaf length or area in many conditions (Fiorani et al. 2000; Bultynck et al. 2004) as also suggested by co-localization of QTLs for final leaf length and elongation rate (Reymond et al. 2004; Ter Steege et al. 2005).

**TEMPORAL AND SPATIAL PATTERNS OF GROWTH AS AFFECTED BY ENVIRONMENTAL STRESSES IN DICOTYLEDONOUS LEAVES**

Leaf expansion in dicotyledonous is often described by three developmental phases, reported as the proliferation phase, the expansion phase and the maturation phase (Fig. 2a, see also Beemster et al. 2005). In contrast to the case in monocotyledonous leaves, those three phases are restricted neither spatially to a determinate leaf zone nor temporally to a precise developmental phase. They coexist within the leaf during a large part of its development with a tip-to-base gradient (Fig. 2b,c). Zones at the tip of the leaf shift from one phase to another before those at the base. During the first phase, tissue area increases exponentially with time, with a nearly constant cell area suggesting that both cell division and tissue expansion are exponential and coordinated (Milthorpe & Newton 1963; Dale 1964; Denne 1966; Poethig & Sussex 1985). During the second phase, cell division progressively slows down and eventually stops, although tissue expansion remains at a maximal relative rate. This results in an increase in the individual cell area (Maksymowych 1973; Pyke, Marrison & Leech 1991; Donnelly et al. 1999). Finally, tissue expansion slows down and ceases, but later in time than cell division in each zone (Avery 1953; Poethig & Sussex 1985; Wolf, Silk & Plant 1986; Granier & Tardieu 1998; Schmudtt et al. 1998; Wiese et al. 2007).

Leaf area is affected by environmental stresses whenever the stress is imposed during one of those three phases. Stresses of similar intensity and duration have the largest effect on final leaf area when they occur during the first phase of leaf development, although relative leaf expansion rate is maximal (Yegappan et al. 1980; Lecoeur et al. 1995; Alves & Setter 2004). Reductions in leaf area during this early stage have a long-term after-effect both on absolute leaf expansion rate during later phases of development and on final leaf area (Lecoeur et al. 1995; Alves & Setter 2004). For instance, a short water deficit during the early period of exponential expansion in leaves of pea or sunflower affects absolute leaf expansion rate 1 or 2 weeks after re-watering of the plants (Lecoeur et al. 1995; Granier & Tardieu 1999a). In the same way, a temporary reduction in incident light during the same early period affects expansion rate of sunflower leaves until the end of leaf expansion (Granier & Tardieu 1999b). This is characteristic of an exponential behaviour in which absolute leaf expansion rate at a given

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**Figure 2.** Schematic representation of the 3 developmental phases occurring in each zone of leaf during dicotyledonous leaf development (a) and of the spatial distribution of these three phases at one stage during leaf development (b for the spatial distribution of relative expansion rate, RER & c for the spatial distribution of relative cell division rate, RDR). Numbers in (a) indicate the different phases of leaf elongation and vertical lines indicate the transition from a phase to the next one. The scales in b and c represent the extent of relative expansion rate and cell division rate in each zone, from data on sunflower leaf development modified from Granier & Tardieu (1998). During the first phase, both expansion and cell division are exponential and at maximal rates (phase 1 in a, base of the leaf in b and c). Then, relative cell division rate decreases with time whereas relative expansion rate is maintained (phase 2 in a, middle of the leaf in b and c). Finally, relative expansion also decreases with time and stop a few days after the end of cell division (phase 3 in a, tip of the leaf in b & c).
time depends on the leaf area at that time. As a consequence, absolute leaf expansion rate measured on a given day depends on environmental conditions experienced by the plant long before the considered day, in contrast to the rapid and short-term effects experienced by monocotyledonous leaves.

The duration of leaf expansion can also be affected by environmental cues. Reduced incident light or soil water content causes a decrease in leaf size, a decrease in maximal absolute leaf expansion rate, but the duration of leaf expansion is either increased or maintained (Rawson & Turner 1982; Rawson & Dunstone 1986; Granier & Tardieu 1999a,b). In a few examples, the decrease in leaf expansion rate is compensated for by the increase in duration of leaf expansion in such a way that final leaf area is not affected by these environmental conditions (Aguirrezabal et al. 2006; Cookson, Radziejewski & Granier 2006). Decreasing day-length also causes a decrease in leaf expansion rate, accompanied by an increase in the duration of leaf expansion with a nearly total compensation in Arabidopsis thaliana (Cookson et al. 2007). In the same way, only measurements of dynamic leaf growth variables could reveal the phenotypes of transgenic plants over-expressing the D-type cyclin, CycD2, which do not show visible phenotypic differences at maturity but have accelerated rates and reduced durations of growth (Cockcroft et al. 2000).

The developmental framework in dicotyledonous leaves is hence characterized by: (1) the absence of a phase with constant absolute leaf expansion rate; (2) quantitatively important after-effects of environmental changes on absolute leaf expansion rate; and (3) appreciable changes in the duration of leaf expansion. The dynamic variables underlying leaf area, namely the rate and the duration of expansion, are more plastic than final leaf area itself with – in some cases – partial or complete compensations between rate and duration when plants are exposed to environmental changes.

The assumed independence of cell number and cell area has been used to model leaf growth as a function of cell production rate in monocotyledonous (Arkebauer & Norman 1995) and dicotyledonous leaves (Lecoeur, Wery & Sinclair 1996). In these models, any increase in leaf area at any time and region of the leaf, is calculated as the product of a new cell number by cell area. In this view, growth depends on cell division in a first period (for dicotyledonous) or in the proximal zone of the leaf base (for monocotyledonous), and on cell expansion in the following period or zone. This is consistent with experimental data reporting that in younger leaves, inhibition of cell division results in fewer cells per leaf, whereas leaf area is reduced with reduction of mature cell size in leaves that are no longer engaged in cell division (Yegappan et al. 1980; Randall & Sinclair 1988; Alves & Setter 2004). In pea leaves, this model adequately predicts the cumulative effect of water stress (Lecoeur et al. 1995).

In other situations, cell division and individual cell expansion cannot be considered as independent processes that contribute by their product to the changes in whole leaf expansion. An alternative model has been proposed by Green (1976), in which environmental cues affect cell division rate and whole leaf expansion rate, whereas their effects on individual cell area are the consequences of the two former effects. The complex spatial and temporal patterns of leaf expansion, cell division and cell size have been simulated adequately using this model in sunflower leaves (Granier & Tardieu 1999a). The model predicts that environmental changes have no effect on final cell area during the early phases of leaf development (or in basal zones of a leaf), when relative leaf expansion rate and cell division rate are affected to the same extent. They have a maximum effect on cell area when they occur later in leaf development (or in more distal zones), when leaf expansion rate is still at a maximum, but cell division rate has started to decrease and is therefore less affected by environmental cues. Consistent with this model (but not with the model stating an independence of cell number and cell area), environmental changes can cause an increase in cell area when the effect of environmental cues on cell division rate is greater than that on whole leaf expansion rate. This is the case, for example, in basal zones of maize, or subjected to water deficit treatments (Tardieu et al. 2000) or nutrient deficiency (MacAdam et al. 1989; Assuero et al. 2004), and in leaves of dicotyledonous species grown with very low incident light during early development (Cookson & Granier 2006).

Genetic or physiological arguments also plead in favour of a model in which leaf growth changes do not depend on independent effects on cell division and individual cell expansion. Support has come from cell cycle mutants in which a slower cell cycle results in larger cells (Hemerly et al. 1995; De Veylder et al. 2001), or in which a more rapid cell cycle results in smaller cells (Dewitte et al. 2003). Recently, a QTL analysis combined with a path analysis has shown that the product of both cell number and cell size does not control individual leaf expansion. These two processes are under the control of more integrated traits,
namely whole-leaf expansion and the number of leaves produced by the plant (Tisné et al. 2008). Other examples in literature suggest the partial dependency of cell number on the number of leaves produced by the plant and the partial dependency of cell area on the date of flowering (Ashby 1948; Wilson 1966; Ter Steege et al. 2005; Cookson et al. 2007).

Our conclusion is that cell size and cell number are at least partially controlled by whole-tissue expansive growth and by leaf production. This has important consequences not only for phenotyping and modelling but also for the genetic development of strategies to increase leaf growth:

1 First, because it suggests that it is acceptable to characterize changes in growth rate with environmental conditions without any measurement of cell number or cell size. Expansive growth is considered, in this view, as a consequence of turgor as influenced by water fluxes in the plant (Bouchabké et al. 2006) and of cell wall properties as influenced by expansins, xyloglucan endotransglycosylases or hydroxyl radicals (Cosgrove 2005).

2 Second, because models can simulate the effect of environmental conditions on leaf expansion without a preliminary intermediate simulation of both cell number and cell size. Such simulation models without considering cell number and size have accounted for the effect of temporal water deficit on the time course of sunflower and maize leaves (Granier & Tardieu 1999a; Chenu et al. 2008). They allowed simulation of the combined effects of environmental conditions and of QTL alleles on the responses of maize leaf growth rate to temperature, evaporative demand and soil water deficit (Reymond et al. 2003).

3 Third, because attempts to increase leaf size by genetic engineering of cell division or expansion may fail. If these two variables are controlled by whole leaf and whole plant processes, their impact on leaf growth itself is expected to be limited, consistent with many experimental results.

SCALING UP FROM CHANGES IN INDIVIDUAL LEAF AREA CAUSED BY ENVIRONMENTAL CUES TO CHANGES IN WHOLE PLANT LEAF AREA

The final profile of leaf area along the plant stem can be divided in three zones, with a common pattern for different species (Fig. 3d). In the oldest, most basal leaves, leaf area increases with leaf position on the stem, intermediate leaves have a maximum area and the youngest, most apical leaves decrease in area with their position on the stem. This characteristic profile is reported for many non-ligneous species such as the sunflower (Dosio et al. 2003), broad bean (Karamanos, Elston & Wadsworth 1982), pea (Lecoeur et al. 1995), maize (Fig. 3d, Chenu et al. 2008) or Arabidopsis.

Figure 3. Development of successive maize leaves, final profile of leaf length and effect of an early soil water deficit. (a) Change with time in predawn leaf water potential in well-watered (continuous line) and water-deficit (filled circle, dots) treatments. Observed data in the well-watered treatment are not shown for better legibility. Error bars, standard deviations. (b) Simulated timing of leaf development as a function of leaf rank with two developmental phases: when the lamina is within (thin line) or outside (thick line) the whorl. (c) Reduction in leaf length between well-watered and water deficit treatments as a function of leaf rank. Bars = observed data; lines = simulated data. (d) Corresponding profile of final leaf length in plants grown in the well watered treatment (open symbols) and the water deficit treatment (closed symbols). Leaves number 6 to 8 were in the phase of rapid leaf elongation when the water deficit treatment was the most severe. As a consequence, those leaves were the most affected by the treatment, as predicted by the model. In contrast, leaf number 12, grown in well-watered conditions, was not affected by the water deficit period that occurred before its phase of rapid elongation. Modified from Chenu et al. (2008).
 depending on the species, this pattern has been related to differences in the rate of leaf expansion between the successive leaves of a plant (Gallagher 1979; Bultynck et al. 2004; Cookson et al. 2007), or to differences in both rate and duration of leaf expansion (Dosio et al. 2003; Bultynck et al. 2004). It is often interpreted via the temporal positions of the development of each leaf in relation to the development of reproductive organs. The first leaves undergo their early development without effect of reproductive organs, which are not growing yet. Later, leaves undergo an increasing influence from reproductive organs (competition for assimilates or signalling), causing a decrease in individual leaf expansion rate and/or duration of expansion. In some genotypes or environmental conditions, the third part of the profile is not observed and the leaf area increases with position on the stem until a maximal leaf area is reached for the last leaf formed (Bultynck et al. 2004 for three Aegilops and two Triticum species; Cookson et al. 2007 for Arabidopsis thaliana Col-0 and Ler accessions grown in long-days).

The profile of a final individual leaf area can be affected by environmental changes in two ways: an effect on the number of leaves produced by the plant or an effect on individual leaf expansion. Leaf number is often unaffected by water or light treatment that affect the whole plant leaf area (Karamanos et al. 1982; Pigliucci, Whitness & Schlichting 1995; Pigliucci & Kolodynska 2002; Aguirrezabal et al. 2006). However, both the whole plant leaf area and the individual leaf area are affected differently by environmental cues in some cases. For example, changes in day-length that reduce whole plant leaf area cause a reduction in leaf number in Arabidopsis thaliana, whereas individual leaf area is slightly increased when the same leaf position is compared (Cookson et al. 2007).

Functional-architectural models have been developed to represent the dynamics of whole plant leaf area expansion by the successive coordinated dynamics of individual leaf expansion (Fournier & Andrieu 1998; Chenu et al. 2008). They combine a sub-model of the progression with time of the plant developmental stages with a sub-model of individual leaf expansion and, in the case of Chenu et al. (2008), a whole-plant model which simulates the feedback of leaf growth on the carbon and water status of the plant via its effects on light interception and transpiration. The first sub-model is based on temporal data that defines the dates of the main transitions in the development of each successive leaf developmental stage for each successive leaves of a plant. Because the duration of each individual phase is defined by temperature-compensated time, this sub-model, at the whole plant level, is often expressed on a thermal time basis (Fig. 3b modified from Hodgest & Evans 1992; Turc & Lecoeur 1997; Dosio et al. 2003; Chenu et al. 2008). It can also be modified in response to light or day-length (Warrington & Kanemasu 1983; Kirby 1995). The second sub-model is usually established from relationships between individual leaf expansion rate (and/or duration)

Figure 4. A conceptual model of the control of individual leaf area with the link between cellular processes (grey text), leaf expansion processes (green text) and whole plant processes (brown text). Solid arrows refer to the functional links between variables within or between scales. Dashed arrows refer to duration of processes, namely leaf production and leaf expansion. Modified from Cookson, Van Lijsebettens & Granier (2005) with experimental results from Ashby (1948), Wilson (1966), Ter Steege et al. (2005), Cookson et al. (2007), Tisné et al. (2008).
and environmental changes that have been obtained on a leaf at a given position on the stem and can be extended to other leaves (Dosio et al. 2003; Bultynck et al. 2004; Chenu et al. 2008). The first two sub-models take into account changes in the timing and rate of individual expansion imposed by reproductive development and whole-plant controls discussed above. Their combination with an environmental scenario (Fig. 3a) can efficiently predict the environmental conditions sensed during the growth of each leaf on the stem (Fig. 3c,d).

Scaling up from changes in individual leaf expansion to changes in whole plant leaf area is therefore possible, but only if data obtained for an individual leaf are coupled with a whole plant developmental model including characterization of developmental stages at each nodal position on the plant and the occurrence of reproductive events that can interfere with individual leaf development. Whole plant leaf area development is then more complex than the product between leaf number and individual leaf expansion.

CONCLUSIONS

Even if strong correlations have been reported in the literature between final leaf area and underlying leaf growth variables, such as leaf expansion rate or epidermal cell number, multi-scale spatial and temporal phenotyping has revealed that the leaf growth changes at a given scale cannot be directly inferred from a lower scale or easily scaled up to the whole-plant level. It highlights that cellular, whole plant or temporal controls can lead to compensations, apparently complicating whole-plant analysis, as it cannot be deduced in a straightforward manner from individual mechanisms (Fig. 4). However, phenotyping and modelling approaches provide evidence that in many cases, a given scale can be ignored because of compensation mechanisms between processes. The integrated leaf-growth phenotype can thus be largely simplified and simulated by a limited number of leaf-growth variables and a limited number of parameters.

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