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Is there a trade-off for C-resources allocation between growth and polyphenol accumulation in tomato under contrasted situations of carbon and nitrogen availabilities ?

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Abstract. Growth and defense are competing plant processes that rely on organic compound syntheses mainly from carbon skeletons and nitrogen assimilates. Therefore, carbon (C) and nitrogen (N) availability in plant organs is crucial to sustain the cost of their concomitant upraising.

We attempted to study in tomato leaves how C and N availability affects growth, C and N status and concentrations of the main primary and C-based secondary (i.e. defensive) metabolites. We compared mature to developing leaves because they exhibit contrasted source-sink activities during ontogeny.

Greenhouse tomato plants were grown hydroponically at two contrasting atmospheric CO₂ concentrations (350 and 700 ppm) and at two contrasting levels of N availability (limiting and non-limiting for plant growth). Five weeks after sowing, we sampled the leaves and determined dry biomass and the concentrations of C, N, free carbohydrates, starch, chlorogenic acid, rutin, kaempferol-rutinoside and lignin.

The concentrations of defense-related compounds were positively correlated with C/N ratio in both leaf classes. These compounds get concentrated under LN, suggesting that these plants invested extra C and N resources in the leaves for the production of defense-related secondary compounds. The starch concentration followed the same pattern in both leaf classes. C and N availability had no effect on free carbohydrates concentration in fully developed leaves. The concentration of lignin, a structural secondary metabolite, was not affected by C and N resource availability, whatever the leaf class.

The results suggest that nutrient fertilization could be a tool to alter the trade-off between growth and defense for nutrient resource allocation. Since the concentration of defense-related compounds in young leaves exceeds that of mature leaves, it is expected that developing leaves, especially under low N, will be able to defend better against predators.

Introduction. Growth and defense are two major plant functions, competing for resource allocation. The former is mostly governed by the major pathways of primary metabolism while an important part of the latter relies on secondary metabolism [1]. Since a single carbon source (photosynthesis) fuels both metabolisms [2], plants must face an endless dilemma. On the one hand, intensive growth provides for competitiveness, but on the second hand, plant defence may benefit from enhanced syntheses of secondary metabolites [1]. If this premise is true, nutrient resource availability is therefore central in plants' life. Among nutrients, carbon (C) and nitrogen (N) are the two elements required in largest quantities by plants and their restrictions limit the syntheses of both primary and secondary metabolites since their composition is greatly dependent on both elements.

Common agricultural practices (N fertilization, CO₂ enrichment in greenhouses ...) often place plants under contrasted carbon and nitrogen availabilities although little is known about their concomitant effects on a range of plant processes that rely on primary and secondary metabolisms. For the former, it is acknowledged that the precise monitoring of crop N status is a powerful tool to attain optimal growth [3]. For the latter, several hypotheses such as the GDB theory [4] have suggested that plants with high C/N status may exhibit larger defensive capacity against pests, suggesting that N fertilization could be a practical leverage to lower pesticide use in agriculture, in accordance with popular wishes for more environmental friendly agricultural practices. The present study reports a greenhouse experiment where tomato plants were grown hydroponically at contrasted N and C availabilities. Plant primary metabolism was characterized by dry weight, soluble sugars and starch accumulations. Secondary metabolism was assessed by the quantification of several phenolics, which are reported to be the main C-based secondary metabolites in tomato leaves [5] and involved in defense. Indeed, chlorogenic acid, a hydroxycinnamic derivate, rutin and kaempferol-rutinoside (KR), two glycosylated flavonoids, are known to inhibit the development of pests [6,7,8]. We also quantified the concentration of lignin which acts in defense the role of a physical barrier for pests. Our goal was to find correlations between processes, in particular for leaves (developing vs. fully developed), since these organs are either sources or sinks for C and they represent important sites for pest attacks.

Materials and Methods. Tomato plants were raised hydroponically in two greenhouses maintained either at ambient CO₂ concentration (LC) or enriched at 700 vpm (HC). The plants were supplied with one of two N-contrasted full nutrient solutions, either low-N (LN, 0.1 mM) limiting plant growth or high-N (HN, 7 mM) non-limiting. Each solution contained either nitrate or a [70:30] nitrate:ammonium mixture. Five weeks after sowing, plants were sampled. Developing and mature leaves were analyzed for dry biomasses, leaf area, C and N concentrations, primary (soluble carbohydrates and starch) and several secondary (chlorogenic acid, rutin, kaempferol-rutinoside and lignin) metabolite concentrations.

Results and discussion. Growth parameters responded as expected, to C and N availabilities. Indeed, LN plants had lower dry weight (DW) and shoot/root ratio than HN plants. Total plant DW decreased by 2.8 folds between HN (NO_3NH_4) nutrition under HC and LN (NO_3NH_4) nutrition under LC. Moreover, the specific leaf area, which is used as an indicator of the leaf thickness, was the lowest in LN and under HC.

LN tomato leaves exhibited higher concentrations of chlorogenic acid, rutin and KR than HN plants. CO_2 concentration had less effect than N, only fully developed leaves being impacted: CO_2 enrichment increased chlorogenic acid concentration under LN and to higher KR concentration at both N availabilities. Lignin concentration was not affected by the treatments. Chlorogenic acid, rutin and KR have been described to play a role in plant defense, whereas lignin is a structural secondary metabolite, and possibly an end-product of the phenylpropanoid biosynthesis chain pathway. Our data could suggest therefore, that under situations where resources are limited, the tomato plants favor the production of defensive metabolites, not of all C-based secondary compounds. This remains, however, a working hypothesis since only lignin concentration was analyzed. Moreover, it remains also possible that C and N resource availabilities modify the composition and quality of lignin, thus altering defense. Whatever the leaf development status, lignin concentration was higher than that of defense-related compounds (1 to 3% in DW instead of less than 1% in DW). Phenolics concentrations in developing leaves were greater than in ageing leaves. Concentrations of secondary metabolites are often highest in immature leaves and decline in mature leaves [9]. By this process, young leaves that are sites particularly sensitive to predators, acquire a higher potential capacity to defend.

The carbon and nitrogen plant status responded to the different environmental conditions. Indeed, the C/N ratio of fully developed leaves was highest in LN plants and in plants grown under HC. Both mature and young leaves responded significantly to N nutrition and CO_2 treatment. Leaves C/N ratio and dry weight were negatively correlated ($R = -0.65$ *** in fully developed leaves, Table 1.A.; $R = -0.67$ *** in developing leaves Table 1.B.). The concentration of the three C-based secondary metabolites correlated with the C/N ratio (*** in mature leaves, Table 1.A.; *** in developing leaves, Table 1.B.).

Starch concentration correlated to C/N ratio ($R = 0.91$ *** in mature leaves, Table 1.A.; $R = 0.92$ *** in developing leaves, Table 1.B.). Starch, is known to be one of the molecules used by plants to store resources when they face stress conditions. Free carbohydrates concentration in young leaves decreased with increasing N availability but in mature leaves (i.e. acting as C-source organs) it was influenced neither by C nor N availability.

Controlling nutrient availability appears as an agronomic leverage for stimulating plant defense, especially by enhancing organ concentrations of low molecular weight secondary compounds such as phenolics.

A		0 '****' 0.001 '***' 0.01 '**' 0.05 'ns' 1							
Characteristics	C:N ratio	Dry weigh	[Starch]	[free carbohydrates]	[Chlorogenic acid]	[Rutin]	[KR]	[Lignin]	
C:N ratio	1	22 ⁽²⁾	22 ⁽³⁾	22 ⁽³⁾	22 ⁽²⁾	22 ⁽²⁾	22 ⁽²⁾	22 ⁽²⁾	
Dry weigh	-0.65 ***	1	22 ⁽³⁾	22 ⁽¹⁾	22 ⁽²⁾	22 ⁽²⁾	22 ⁽²⁾	22 ⁽¹⁾	
[Starch]	0.91 ***	-0.51*	1	22 ⁽³⁾	22 ⁽³⁾	22 ⁽²⁾	22 ⁽²⁾	22 ⁽³⁾	
[free carbohydrates]	ns	ns	ns	1	22 ⁽³⁾	22 ⁽³⁾	22 ⁽³⁾	22 ⁽¹⁾	
[Chlorogenic acid]	0.84 ***	-0.63 ***	0.74 ***	ns	1	22 ⁽²⁾	22 ⁽²⁾	22 ⁽²⁾	
[Rutin]	0.77 ***	-0.41 *	0.73 ***	ns	0.90 ***	1	22 ⁽¹⁾	22 ⁽¹⁾	
[KR]	0.85 ***	-0.54 **	0.82 ***	ns	0.92 ***	0.95 ***	1	22 ⁽¹⁾	
[Lignin]	-0.44 *	ns	ns	ns	ns	ns	ns	1	
B		0 '****' 0.001 '***' 0.01 '**' 0.05 'ns' 1							
Characteristics	C:N ratio	Dry weigh	[Starch]	[free carbohydrates]	[Chlorogenic acid]	[Rutin]	[KR]	[Lignin]	
C:N ratio	1	19 ⁽¹⁾	20 ⁽²⁾	20 ⁽²⁾	20 ⁽¹⁾	20 ⁽³⁾	20 ⁽²⁾	20 ⁽¹⁾	
Dry weigh	-0.67 ***	1	19 ⁽¹⁾	19 ⁽¹⁾	19 ⁽¹⁾	19 ⁽¹⁾	19 ⁽¹⁾	19 ⁽¹⁾	
[Starch]	0.92 ***	-0.58 **	1	20 ⁽²⁾	20 ⁽³⁾	20 ⁽³⁾	20 ⁽¹⁾	20 ⁽¹⁾	
[free carbohydrates]	0.79 ***	-0.59 **	0.77 ***	1	20 ⁽¹⁾	20 ⁽²⁾	20 ⁽¹⁾	20 ⁽³⁾	
[Chlorogenic acid]	0.77 ***	-0.80 ***	0.70 ***	0.50 *	1	20 ⁽¹⁾	20 ⁽²⁾	20 ⁽¹⁾	
[Rutin]	0.86 ***	-0.71 ***	0.78 ***	0.58 **	0.95 ***	1	20 ⁽³⁾	20 ⁽¹⁾	
[KR]	0.95 ***	-0.79 ***	0.81 ***	0.80 ***	0.86 ***	0.87 ***	1	20 ⁽¹⁾	
[Lignin]	ns	ns	ns	ns	ns	ns	ns	1	

Table 1: Correlations between parameters in fully developed leaves (A) and in developing leaves (B). Correlations were measured on individual values. In the bottom part of tables, numbers are the correlation coefficients R of Pearson or Spearman.

In the top part of tables, degree of freedom and superscript indicates types of correlation realized: (1): Pearson – (2): Pearson with log-transformed variable – (3): Spearman

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