

Effects of *Globodera rostochiensis*, water stress and exogenous abscisic acid on stomatal function and water use of Cara and Pentland Dell potato plants

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SUMMARY

Infection with *Globodera rostochiensis* increased stomatal resistances and decreased water use of both Cara (resistant, tolerant) and Pentland Dell (non-resistant, intolerant) potato plants. Exogenous abscisic acid (A.B.A.) increased both of these effects : it increased stomatal resistance of Pentland Dell severalfold but only for two days, whereas the increase was smaller in Cara but lasted for about six days. Water stress also increased stomatal resistance and decreased water use with the greater effects on Cara, probably because Cara plants were bigger than those of Pentland Dell and exhausted the water reserves in their pots more quickly. Measurements show that Cara may contain up to nine times the concentration of A.B.A. in its leaves as Pentland Dell subjected to the same treatments, but that the proportional changes in A.B.A. content caused by nematode infection and water stress are greater in Pentland Dell. Stomatal function was assessed on epidermal peels of the two cultivars bathed in a range of concentrations of calcium chloride solution and illuminated for three hours : nematode infection had no effect on stomatal apertures but mean stomatal apertures were greater in Pentland Dell than Cara.

RÉSUMÉ

Effets de Globodera rostochiensis, du stress hydrique et de l'acide abscissique exogène sur le fonctionnement des stomates et l'utilisation de l'eau chez les cultivars Cara et Pentland Dell de la pomme de terre

L'infestation par *Globodera rostochiensis* accroît les résistances des stomates et diminue l'utilisation de l'eau chez les deux cultivars Cara (résistant, tolérant) et Pentland Dell (non résistant, non tolérant) de la pomme de terre. L'acide abscissique exogène (A.A.E.) renforce ces deux effets : il augmente de plusieurs fois la résistance stomatique chez « Pentland Dell », mais seulement pendant deux jours; cette augmentation était plus faible chez « Cara », et ne se produisait que pendant six jours. Le stress hydrique accroît lui aussi la résistance stomatique et diminue l'utilisation de l'eau, ces effets étant plus prononcés chez « Cara », probablement parce que les plants de ce cultivar étaient plus grands que ceux de l'autre et de ce fait épuisaient plus rapidement la réserve en eau des pots de plantation. Des mesures ont montré que « Cara » peut présenter dans ses feuilles une concentration en A.A.E. allant jusqu'à neuf fois celle des feuilles de « Pentland Dell » soumis aux mêmes traitements, mais que, proportionnellement, les modifications du taux d'A.A.E. provoquées par le nématode et le stress hydrique sont plus importantes chez « Pentland Dell ». Le fonctionnement des stomates a été établi sur des lambeaux d'épiderme baignant dans une série de solutions de chlorure de calcium de concentrations graduées, le dispositif étant éclairé pendant trois heures : l'infestation par le nématode n'a aucun effet sur l'ouverture des stomates, mais l'ouverture stomatique moyenne était plus grande chez « Pentland Dell » que chez « Cara ».

Water stress in plants leads to closure of stomata (Epstein & Grant, 1973), which decreases both transpiration and photosynthesis in potato plants (Zelitch, 1971; Shekhar & Iritani, 1979). Compared to other species, the potato is a drought sensitive plant, and it is generally agreed that there are varietal differences in resistance or tolerance to water stress (Harris, 1978).

Little experimental evidence is available concerning the factors causing these differences in reaction to water deficit. Factors that could be involved include morphological structure, stomatal behaviour (Van Loon, 1981) and hormonal changes in the plants. Ageeb (1968) found

that the differences in drought tolerance between King Edward and Majestic could partly be explained by differences in rooting depth and root extension. Van Loon (1981) reported that, at flowering, the most drought tolerant cultivar had the deepest and the most drought sensitive cultivar the shallowest root system. Epstein and Grant (1973) found that stomatal diffusion resistances of the cultivar Russet Burbank were two to three times greater than those of Katahdin under conditions of water stress, even though the relative water content of leaves was similar in the two cultivars. Van Loon (1981) also reported that there were marked

differences between cultivars in stomatal response under dry conditions : the drought tolerant cultivar Bintje closed its stomata earlier than the drought sensitive Saturna.

There are also reports that nematodes increase stomatal resistances of their hosts. Evans, Parkinson and Trudgill (1975) reported that stomatal resistances of Pentland Dell infected with many potato cyst nematodes were much greater than those of lightly infected plants. Maris Piper also showed similar trends but with greater stomatal resistances than Pentland Dell during water stress periods. Kaplan, Rohde and Tattar (1976), working on the effects of small numbers of lesion nematodes, *Pratylenchus penetrans*, on sunflower, found that infected plants showed increased diffusive resistance in advance of healthy plants growing under similar conditions. The work of Meon (1979) provided more evidence, as infestation with *Meloidogyne javanica* increased the resistance to diffusion of water vapour from stomata of tomato plants.

The closure of stomata during water stress conditions is necessary to reduce transpiration, and this is achieved by the transmission of a "distress signal", abscisic acid (A.B.A.), from the mesophyll chloroplasts to the guard cells of the stomata (Wright, 1969; Wright & Hiron, 1969). The reports on effects of nematodes on A.B.A. content of leaves in relation to stomatal opening are very few. Parasitism of peach by *Macroposthonia xenoplax* caused aberrant fluctuations of A.B.A. in shoot tissue (Nyczepir & Lewis, 1980). Evans (1982 *a*) reported that, of the four he tested, the potato cultivar most tolerant of cyst nematodes had the greatest A.B.A. concentration when uninfected and showed the smallest increase when infected.

Hence the question arises that if nematodes induce the symptoms of water stress in plants by raising A.B.A. levels, closing stomata and reducing transpiration, then would the morphological, hormonal and other characteristics which enable drought tolerant plants to withstand water stress also enable plants to tolerate nematode attack? This paper examines three questions : *i*) the comparison between the effect of water-stress and nematode-stress on two potato cultivars tolerant and intolerant of *Globodera rostochiensis*; *ii*) whether the use of exogenous A.B.A. as an antitranspirant would reduce stomatal opening of infected plants and increase water use efficiency and *iii*) whether increased levels of A.B.A. or calcium (Evans, 1982 *a*; Fatemy & Evans, 1983) in the infected plants are responsible for the reduction of transpiration (calcium has been reported to have an inhibitory effect on stomatal opening, Fischer, 1968; Willmer & Mansfield, 1969).

Materials and methods

The cultivars used were Cara (resistant to and tolerant of *G. rostochiensis*) and Pentland Dell (non-resistant and

intolerant). Tuber pieces with single sprouts and weighing 10 g were grown in 12.5 cm plastic pots filled with 1,000 g of sterilised sandy loam. When nematodes were included half the soil was added to the pot, sufficient cysts of *G. rostochiensis* Rol were added to give 250 eggs/g soil overall and the pot was then filled with the remainder of the soil. Seven grammes of slow-release fertiliser (18 % N, 11 % P, 10 % K) were added and 100 g of polyethylene granules poured on the soil surface to minimise water loss. The moisture content was maintained at about field capacity by weighing and making up to a constant weight with distilled water. The constant weight was increased at regular intervals by an amount corresponding to the water content of the plant. Four replicates per treatment were used. The water-stress treatment was applied to four uninfected plants of each cultivar by withholding watering, starting 43 days after planting, for 5 days.

Abscisic acid was applied to four infected plants of each cultivar on four occasions : 40, 42, 44 and 46 days after planting. On each occasion 5 mg of A.B.A. (all trans), dissolved in 5 ml water, was injected into the soil, as close to the roots as possible, at four points in the pot. The stomatal resistance of the under surface of the terminal leaflet of the fifth fully expanded leaf from the apex was measured with a porometer (Parkinson & Legg, 1972) every day starting from 39 days after planting. All of the leaflets from this leaf were used for A.B.A. determination on day 47. Leaf samples were wrapped in aluminium foil, immediately frozen in liquid nitrogen and stored at -20° until assay. Their A.B.A. contents were determined by the method of Quarrie (1978).

On day 47, the two sub-terminal leaflets of leaf 10 from the apex were excised from two plants of each cultivar, one nematode-free and the other infected, and pieces of the lower epidermis peeled away (Richardson *et al.*, 1979). The epidermal "peels" were immediately floated in buffer solution (50 mM KCl and 10 mM 4-morpholine-ethane sulphenic acid [MES] adjusted to pH 6.15 with KOH) cuticle side up, in petri dishes. Six peels were added to each of the dishes, which contained buffer solution and a series of concentrations of calcium chloride. The dishes were illuminated from beneath with a light box (intensity 21,000 lux) and carbon dioxide-free air was bubbled through the solution (0.16 dm³/min to each dish). After a 3 h incubation period, three peels were selected at random from each treatment, and ten stomatal apertures were measured on each using a projection head connected to a Vickers M series microscope.

Results

STOMATAL RESISTANCES AND A.B.A. CONTENT

Stomatal resistance (R_s) is the reciprocal of stomatal conductance, which measures the rate of loss of water

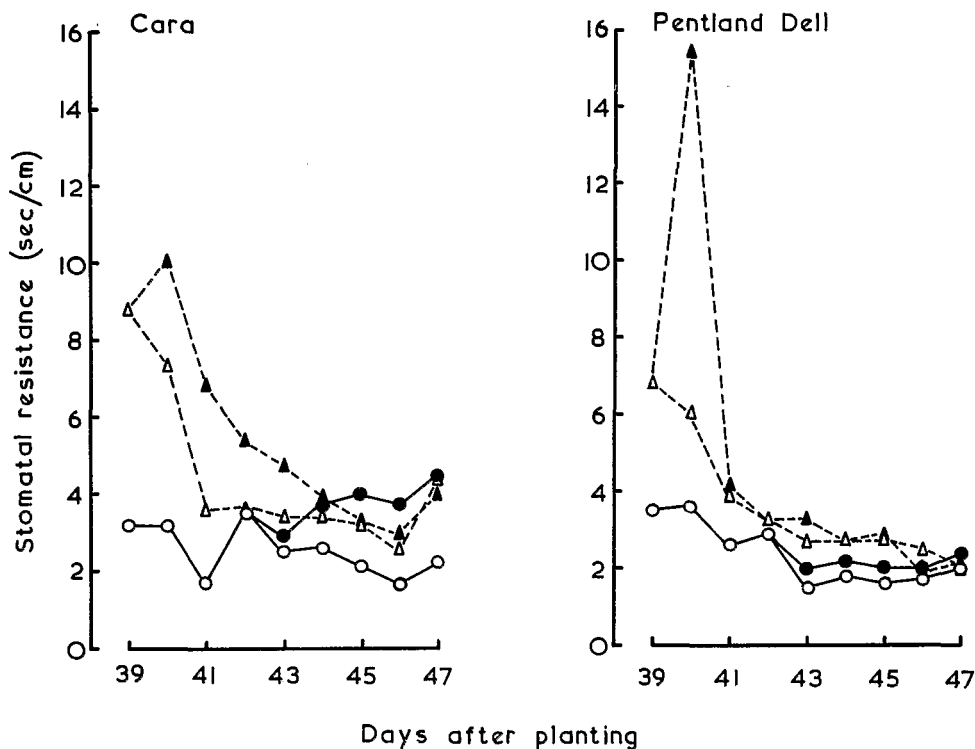


Fig. 1. Stomatal resistances (sec/cm) of Cara and Pentland Dell potato plants 39-47 days after planting (means of four replicates). Plants were - ○ - uninfected and watered normally, - ● - uninfected but water stressed, - △ - infected with *G. rostochiensis* and watered normally, - ▲ - infected with *G. rostochiensis* and treated with A.B.A.

through unit leaf area; R_s is usually expressed in the units of sec/cm. Daily measurements of R_s were taken from 39 days onwards (Fig. 1). Uninfected plants of Cara had slightly smaller R_s than Pentland Dell initially but later they showed slightly higher resistances. Uninfected Cara also had higher A.B.A. concentrations ($P < 0.001$) than uninfected Pentland Dell (9 times the concentration, untransformed data, Table 1). Plants infected with nematodes had increased A.B.A. concentrations (28 % in Pentland Dell compared with 14 % in Cara, untransformed data). However the absolute level for infected plants was higher in Cara than Pentland Dell ($P < 0.001$). This increase in A.B.A. level probably affected stomatal opening, as infected plants had greater stomatal resistances than uninfected plants during this period. Moreover, stomata of infected Cara had higher resistances than infected Pentland Dell although the differences between uninfected and infected plants became less as they grew older.

Mild water stress also increased A.B.A. concentration significantly, in Cara at $p < 0.05$ and in Pentland Dell at $P < 0.001$. Although this increase was greater in

Pentland Dell, stomata of Cara reacted more rapidly to water stress than Pentland Dell in that they showed significantly ($P < 0.01$) higher resistances than well-watered plants from 44 days, with values consistently greater than those of nematode infected plants. Stomatal resistances of water-stressed Pentland Dell plants also increased, but the differences from well-watered plants were not significant.

RESPONSES OF STOMATA TO EXOGENOUS A.B.A.

Infected plants treated with A.B.A. had the highest concentrations of A.B.A. of all, with Pentland Dell showing the larger percentage increase (compared with the infected control), but with Cara showing the greater absolute increase and greater absolute concentration. However, despite the large A.B.A. content of the plants, only the first application (at 40 days) had a marked impact on R_s , with the increase being significant only for Pentland Dell ($P < 0.001$); R_s was measured 5 h after A.B.A. treatment but was not significantly increased in Cara. Furthermore, the next three treatments with A.B.A.

Table 1

Abscisic acid content (ng/g DW) of Cara and Pentland Dell potato plants which were uninfected, uninfected but water stressed, infected with *G. rostochiensis*, or infected and treated with A.B.A.

Cultivar	Treatment	Abscisic acid (ng/gDW)	Log ₁₀ Abscisic acid (ng/gDW + 0.5)
Cara	uninfected	2,810	7.9
	uninfected and water stressed	4,900	8.5
	infected	3,190	8.1
	infected + A.B.A.	7,130	8.8
Pentland Dell	uninfected	308	5.6
	uninfected and water stressed	945	6.8
	infected	393	6.0
	infected + A.B.A.	3,440	8.0
	S.E.D. (Res. df)		0.23 (24)

(on days 42, 44 and 46) had no significant effect on stomatal opening. In fact, there was a sharp decline in R_s of A.B.A. treated Pentland Dell plants and their R_s values became similar to those of the infected control plants; R_s of Cara declined more slowly after the first application of A.B.A.

WATER CONSUMPTION

In general, Cara used more water than Pentland Dell whether infected or not (Fig. 2). Infected plants of both cultivars used less water ($P < 0.05$) than uninfected and when some of these plants were treated with A.B.A., their water consumption decreased even more: the total amounts transpired during days 40–47 were 149 and 106 g for infected Cara and infected Cara treated with A.B.A. respectively, and 70 and 61 g for infected Pentland Dell and infected Pentland Dell treated with A.B.A. respectively. An increase in soil water deficit decreased water consumption of uninfected plants: total amounts used during the stress period were 173 and 101 g for well-watered and stressed Cara respectively and 119 and 81 g for well-watered and stressed Pentland Dell respectively. This reduction in water use following water stress was relatively much greater in Cara than in Pentland Dell but was not related to root weight (see Table 3).

STOMATAL APERTURES

Table 2 shows that increasing calcium chloride concentrations lead to increasing inhibition of stomatal opening in detached epidermis observed after the 3 h treatment period, for both uninfected and infected Cara and Pentland Dell. In fact, there were no obvious behavioural differences in the detached epidermis of leaves from infected or nematode-free plants. However, the overall stomatal apertures of Cara were smaller than those of Pentland Dell.

Table 2

Stomatal apertures (μm) of Cara and Pentland Dell potato plants measured from epidermal peels treated with increasing concentrations of CaCl_2 .

All solutions used were 50 mM KCl and 10 mM MES buffered at pH 6.15. Results are means of 90 measurements.

CaCl_2 concentration	G. rosto- chiensis*	Stomatal aperture ($\mu\text{m} \pm \text{SE}$)	
		Cara	P. Dell
0	—	3.4 (0.1)	5.3 (0.1)
	+	3.6 (0.2)	5.3 (0.1)
0.5 mM	—	1.6 (0.2)	1.9 (0.1)
	+	1.4 (0.2)	1.9 (0.1)
1.0 mM	—	0.8 (0.1)	1.3 (0.1)
	+	0.9 (0.1)	1.2 (0.1)

* : — : Nematode free; + : 250 eggs/g soil *G. rostochiensis* added to each pot.

GROWTH ANALYSIS

Nematode infection significantly ($P < 0.05$) decreased plant size, numbers of leaves and leaflets and final dry weight of above and below ground parts, more for Pentland Dell than Cara (Table 3). Mild water stress had no significant effect on the height or number of leaves of uninfected plants but, although it was only applied for 5 days, it did reduce dry weight. Treatment with A.B.A. decreased the growth of infected plants, more for Cara than Pentland Dell.

Discussion

Infection of potato plants by *G. rostochiensis* was associated with accumulation of A.B.A. in the fifth leaves from the apex. Such an accumulation might be caused by water stress and reduced translocation of water from roots to shoots when transfer cells are formed in response to infection by the nematodes (Meon, Fischer & Wallace, 1978). Similar results were found by

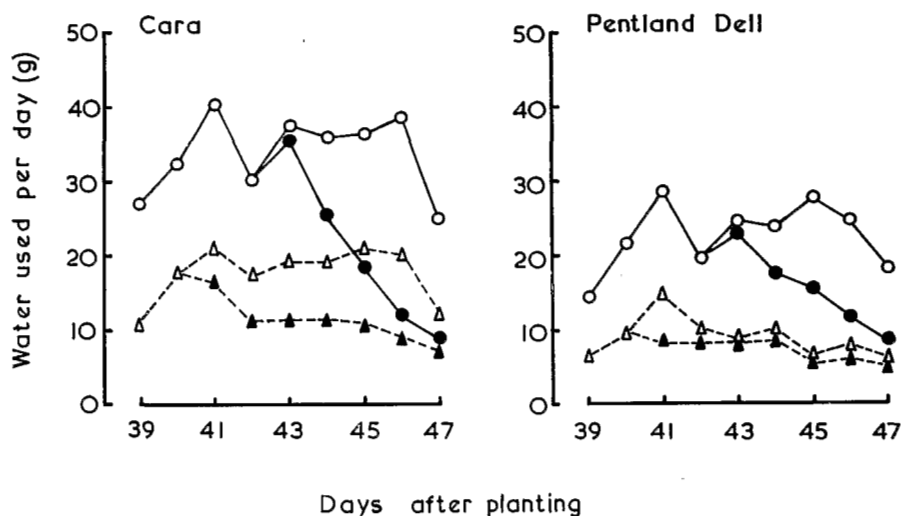


Fig. 2. Daily water use (g) of Cara and Pentland Dell potato plants 39-47 days after planting (means of four replicates). Plants were - ○ - uninfected and watered normally, - ● - uninfected but water stressed, - △ - infected with *G. rostochiensis* and watered normally, - ▲ - infected with *G. rostochiensis* and treated with A.B.A.

Evans (1982 a). Water stress also increased the A.B.A. level in leaves of both cultivars and this probably then decreased transpiration by closing the stomata. Generally, Cara was more responsive to environmental changes than Pentland Dell: its stomata were more closed in the presence of nematodes and they also closed more rapidly than those of Pentland Dell when water stress was applied. Klar and Franco (1979) reported that Maris Piper (a cultivar resistant to *G. rostochiensis*) is more drought resistant than Pentland Dell because of a larger canopy diffusive resistance and higher leaf water potential when growing in infested dry soil. Although Evans (1982 b) found that Pentland Dell showed the largest increase in R_s and Cara the smallest in heavily infested plots 13 weeks after planting, Cara tolerated nematode attack best. This is the opposite of the results in this experiment, but in the field Pentland Dell may have been more water stressed than Cara. Cara has larger tops, a higher transpiration demand, and a more extensive root system than Pentland Dell. Its relative tolerance to *G. rostochiensis* is partly due to its larger root system (which would permit better exploitation of water reserves in the field although, in the confined space of a pot, Cara may have exhausted the water reserves and become more water stressed than Pentland Dell), and partly to its ability to close stomata rapidly, so preventing excessive loss of water and thereby allowing the plant to maintain its turgor. This regulatory mechanism may be mediated by the elevation of A.B.A. levels. This elevation occurred in both cultivars when they were infected

with nematodes or water-stressed. However, the reasons for Pentland Dell, despite its relatively larger increase in A.B.A. levels following both nematode infestation and water stress, not having relatively larger responses in R_s is not understood. Perhaps A.B.A. became rapidly inactivated in Pentland Dell and very slowly in Cara or perhaps Cara needs only a small amount of stress signal (A.B.A.) to close its stomata. Beardsell and Cohen (1975) found in maize that, as water stress developed, stomatal closure began before the level of A.B.A. had risen appreciably in the leaves. This could be due to a redistribution of the A.B.A. that was already present but normally contained within the mesophyll chloroplasts of unstressed plants (Mansfield & Wilson, 1981). A similar mechanism might be the basis for differences between Cara and Pentland Dell and could only be investigated if a method for measuring "active" rather than "total" concentrations of A.B.A. were available.

The effect of A.B.A. application to infected plants was to increase the internal concentration, cause stomata to close and reduce transpiration. The effect was more noticeable in Cara, as its stomata took longer (5 days) to return to their original aperture (i.e. to become as open as those of untreated infected plants, Fig. 1, which is direct evidence for slower inactivation of A.B.A. in Cara). Stomata of Pentland Dell fully reopened as soon as 22 hours after the first application of A.B.A. Infected Cara plants used less water when treated with A.B.A. than the infected controls and their growth was much reduced by the end of the experiment. Improve-

Table 3

Growth measurements at 47 days after planting of Cara and Pentland Dell potato plants which were uninfected, uninfected but water stressed, infected with *G. rostochiensis* or infected and treated with A.B.A.

Treatment	Cultivar	Height (cm)	Leaf No.	Leaflet No.	Shoot DW (g)	Root DW (g)	Shoot/ Root	Total DW (g)	Total water (g)/ Dry weight roots (47 days)
Uninfected	Cara	79.3	18.8	116.3	6.6	0.60	11.1	7.2	1,655
	P. Dell	85.4	18.5	85.8	5.0	0.44	11.5	5.5	1,625
Uninfected and Water-stressed	Cara	74.9	18.8	137.8	5.2	0.55	9.3	5.7	1,587
	P. Dell	77.9	17.3	79.8	4.3	0.40	10.6	4.7	1,653
Infected	Cara	62.9	16.8	93.8	3.6	0.50	7.3	4.1	1,141
	P. Dell	42.0	13.0	46.8	2.0	0.20	10.6	2.2	1,710
Infected + A.B.A.	Cara	58.5	15.5	87.0	2.8	0.38	7.4	3.2	1,418
	P. Dell	40.0	11.8	42.8	1.9	0.17	12.4	2.1	2,005
S.E.D. (Res. df 24)		3.46	0.95	13.48	0.37	0.046	1.43	0.41	
L.S.D. 5 %		7.1	2.0	27.8	0.80	0.09	3.0	0.85	

ment in water use efficiency by causing stomatal closure by applying A.B.A. has been demonstrated experimentally (Jones & Mansfield, 1972; Mizrahi *et al.*, 1974; Raschke, 1976). This improvement in water use efficiency has also been demonstrated in nematode infected plants (Fatemy, unpublished data) especially during early growth when they used less water without their growth being affected. Later on, however, their transpiration ratios either increased or remained smaller but with much reduced growth. The absence of a persistent effect of A.B.A. application in this experiment may be due to a rapid sequestration or inactivation of the exogenous A.B.A. (Cummins, Kende & Raschke, 1971) in the soil or plant. However, the method did demonstrate the inhibitory effect of A.B.A. on stomatal opening and its role in stress conditions.

Results from the detached epidermis peels of leaves showed that there were no apparent behavioural differences of stomata between infected and uninfected plants. This suggests that although levels of calcium may be higher throughout a nematode infected plant, the level of calcium present in the epidermal layer may not be abnormally high, or that the calcium in leaf tissue is largely present in an immobile form such as calcium oxalate, or that there is rapid equilibration of calcium in the epidermal tissue with that in the bathing medium. If the latter explanation is correct then nematode-induced increases in calcium concentration may be responsible for the reduced transpiration of nematode-infected plants. Results from this experiment showed higher A.B.A. concentration in the leaves of nematode infected

plants and yet the stomatal apertures of detached epidermis recorded in Table 2 are the same for both uninfected and infected plants. The 3 h incubation period may have allowed the A.B.A. to diffuse out of all the epidermal peels into the bathing medium so that the only influence on stomatal aperture was the osmotic potential of the medium.

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