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Original Article

Effect of cadaverine on *Brassica juncea* (RH-30) seedlings under multiple stress - A quantitative analysis

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Abstract

Background: Plants, in general, are subject to various kinds of stress, biotic and abiotic, both natural and manmade. Cadaverine (Cad) is a lysine catabolite and is involved in the growth and development of plants. The present study aimed to determine the effects of cadaverine response on the induction of polypeptide profile under multiple stresses in leaf and root tissues of *Brassica juncea*, and to diagnose the changes in gene expression (if any). The protein content was analyzed using SDS-PAGE and the results were further validated using densitometry. The basal medium used for tissue culture was MS medium, formulated with different stress conditions and treatments without and with Cad (100mM NaCl, 1mM Cd or Pb, 5mM NH_4NO_3, 1mM cadaverine). Cad treatment showed increased protein content in the presence of NH_4NO_3, even in seedlings provided/ supplemented with multiple stresses. The protein content was analyzed using SDS-PAGE and the results were further validated using densitometry. Supplementation of Cad induced the expression of 5 more peptides in leaf tissue, such that were not observed in a leaf of the seedling without Cad. Cad enrichment in root tissue did not change the expression of any peptide in NaCl environment, but it was affected in the absence of Cad by saline conditions. The activating performance of Cad in increasing the expression of peptides, and its mitigating the different effects of multiple stresses, suggest its role in growth and development of leaf and root tissues of *Brassica juncea* (RH-30).

Keywords: *Brassica juncea*, Cadaverine, densitometry, polyamines, protein, quantification, stress

1. Introduction

Urbanization and anthropogenic activities have resulted in accumulation of waste materials causing significant unfavorable modifications to the surroundings (Chen, 2007). Accumulation of heavy metals is one such modification, with the escalating toxicity becoming a threat to both the biological system and the environment (Nagajyoti, Lee, & Sreekanth, 2010). Due to the non-biodegradable nature of heavy metals, their enrichment in soil results in their accumulation in exposed plants, ultimately affecting the growth and development of plants. Further, they have been shown to access human population via the food chain, with chronic accumulation in the liver and the kidneys, disrupting biological pathways (Jaishankar, Tseten, Anbalagan, Mathew, & Beeregowda, 2014). Heavy metals induce oxidative stress in plants due to the generation of reactive oxygen species (ROS) leading to stunted growth, necrosis, chlorosis of leaf, poor quality and quantity of fruit; and weakened development of roots, shoots, and leaves (Emamverdian, Ding, Mokhberdoran, & Xie, 2015).

Brassica juncea is a member of Brassicaceae family (Szollosi, 2011). It has an intense flavor and various healing properties (Fomina, 1962). Seed oil is obtained from *B. juncea*, and the crushed seeds are utilized in making mustard. In addition to the vegetable uses, its medicinal role has also been reported (Tomar, Lakra, & Mishra, 2013 a). It has

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diuretic, rubefacient, emetic, and anti-septic properties. Also, it is known to be a repository of valuable vitamins (vitamin A and C) and iron. It also contains calcium, beta carotene, potassium, thiamine, riboflavin, and antioxidants such as carotenes, indoles, flavonoids, zeaxanthin, and lutein (Arena, Cacciola, Dugo, Dugo, & Mondello, 2020).

Cadaverine, a lysine catabolite, is a diamine involved in the growth and development of plants. Lysine decarboxylase (LDC) catabolizes lysine forming an imino compound, i.e., cadaverine. Presence of the enzyme LDC in higher plants, specifically in plants belonging to families Leguminosae, Gramineae, and Solanaceae, implies the wide presence of cadaverine (Tomar, Lakra, & Mishra, 2013a, b). Cadaverine is also present in the environment; it can be produced by rhizosphere and phyllosphere microbes (Jancewicz, Gibbs, & Masson, 2016). Cadaverine is a product of bacterial decomposition, and is malodorous by its nature; due to the cadaverine, cadavers have a foul rotting smell (Kusano, Berberich, Tateda, & Takahashi, 2008). It is involved in numerous activities such being a precursor of polyamides, plays a role in water absorption, ensures the survival of cells in acidic conditions, protects cells that are starved of inorganic phosphate, Pi, under anaerobic conditions, and regulates animal growth (Ma *et al.*, 2017; Moreau, 2007; Samartzidou, Mehrazin, Xu, Benedik, & Delcour, 2003). Further roles include response to stress, cell signaling, insect defense, and in tolerance to salt or heavy metal stress (Jancewicz *et al.*, 2016; Rajpal, & Tomar, 2020).

This study assessed the effects in response to cadaverine on polypeptide profile under multiple stresses in leaf and root tissues of *Brassica juncea*, to diagnose the changes in gene expression, if any.

2. Materials and Methods

2.1 Estimation of total soluble protein and SDS-PAGE analysis

Lowry method was used to estimate the total soluble protein present in leaf and root tissues (Lowry, 1951). Determination of protein quality (protein content) was done by using the standard curve for bovine serum albumin. Protein molecular weights were determined by SDS-PAGE (Laemmli, 1970). Standard protein markers were used for the characterization of molecular weight. Using migration distances, molecular weights of sample proteins were determined.

2.2 Densitometric analysis

For determining quantities of polypeptides separated in the SDS gel, and to ensure accurate data, densitometry was done using a densitometer. The retention time was recorded for each protein band. UV gel documentation and UV gel star MV were used for the density measurements. Depending upon the density of the particular peptide, different graphical peaks were obtained. Densitogram (protein band intensities) was quantified for areal percentages, and variation in protein samples upon treatment was estimated by calculating the protein area.

3. Results and Discussion

3.1 PAGE analysis of proteins

3.1.1 Leaf tissue of 7-day-old seedlings under stress conditions without Cad

A total of 11 bands of polypeptides, namely at 66, 56, 51.8, 50, 40.6, 35, 24.6, 22, 14, 12 and 11 kDa, were observed in leaf tissues of seedlings, out of which the peptides of 66 kDa and 56 kDa were expressed highly (Figure 1). The peptides of molecular weights 35, 14, 12 and 11 kDa disappeared upon saline treatment, whereas the expression of 56 kDa peptide increased a little.

Upon NH_4NO_3 supplementation, more peptides of 90, 88, 85, 80, 75, 51.8, 48 and 44 kDa were expressed. Also, the expression of peptides at 66 and 56 kDa increased and the expression of salt induced peptide at 50 kDa was suppressed by the NH_4NO_3 enrichment. Supplementation of NH_4NO_3 to NaCl stressed plants caused the disappearance of high molecular weight peptides, such as those at 90, 88, 85, 80, 75 and 29.6 kDa, and reduced the expression of peptides at 66 and 56 kDa. The expression of peptides of molecular weights 90, 88, 80, 75 and 50 kDa was induced by Cd treatment over the control, whereas the expression of two more peptides, namely at 85 and 44 kDa, was induced upon Pb treatment over Cad, while the rest of the proteins were same as induced by Cd treatment.

The expression of peptides at 85, 51.8 and 44 kDa was observed for the combination treatment (Cd+NaCl): these were induced as compared to the plants exposed to Cd only. In contrast, there was suppressed expression of peptides at 90, 44, 40.6, 37, 35 and 29.6 kDa for the Pb+NaCl treatment, compared to plants exposed to Pb only.

Further, stress combinations (Metal+ NaCl) were supplemented with NH_4NO_3 so that peptide profiles in leaf tissue can be examined. This resulted in the suppressed expression of peptides at 90, 85, 44, 40, 40.6, 37 and 29.6 kDa in plants exposed to Cd+ NaCl and suppressed expression of peptides at 85, 44, 37 and 29.6 kDa in plants exposed to Pb+ NaCl.

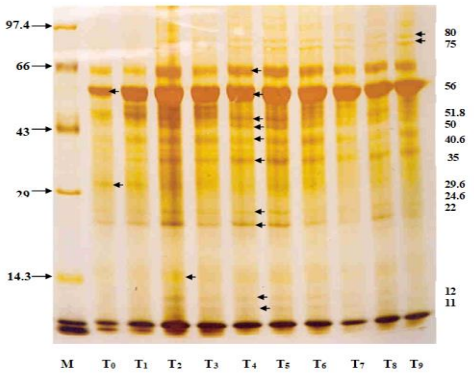

Figure 1. Protein profile of leaf tissue of 7-day-old seedlings under various stress conditions without Cad (M-Marker, T_0- Control, T_1- NaCl (100mM), T_2- NH_4NO_3, T_3- NaCl+ NH_4NO_3, T_4- Cd (1mM), T_5- Pb (1 mM), T_6- Cd+ NaCl, T_7- Pb+ NaCl, T_8- Cd+ NaCl+ NH_4NO_3, T_9- Pb+ NaCl+ NH_4NO_3)

3.1.2 Leaf Tissue of 7-day-old Seedlings under stress conditions with Cad

A total of 16 peptides were observed upon Cad supplementation over control (without Cad) where only 11 peptides observed (Figure 2). The rank order of expression level decreased as follows: 56>60>48.7, 46=44, =39, =34.5, =28, =26, =22>73.8, 68, 31, 14.9, 13, 11.8. The peptides either disappeared, such as those at 73.8 and 60 kDa, or was slightly suppressed like those at 63.8, 48.7, 44, 39, 34.5, 28, 26 kDa; and the remaining peptides showed no change under Cad+ NaCl environment.

No change in the peptide expression was observed upon application of NH_4NO_3 to the plants, but peptides of 73.8 and 68 kDa got suppressed in Cad+NaCl environment (T_3). However, peptide expression did not change upon Cad supplementation to plants stressed with Cd as compared to Cad treatment while no expression was suppressed by metal expressed due to Cad. Plants exposed to Pb also showed a similar response.

Moreover, when metal exposed plants when subjected to saline conditions supplemented with Cad, only the expression of peptide at 13 kDa was suppressed, while the expression of all other peptides remained same in Cd environment. Also, no change in the expression of peptides was observed upon NH_4NO_3 and Cad supplementation to multiple stressed plants (T_8 and T_9).

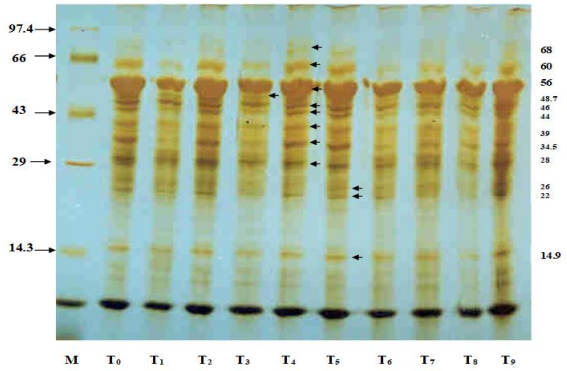

Figure 2. Figure 2 Protein profile of leaf tissue of 7-day-old seedlings under various stress conditions with Cad (M-Marker, T_0- Control, T_1- NaCl (100mM), T_2- NH_4NO_3, T_3- NaCl+ NH_4NO_3, T_4- Cd (1mM), T_5- Pb (1 mM), T_6- Cd+ NaCl, T_7- Pb+ NaCl, T_8- Cd+ NaCl+ NH_4NO_3, T_9- Pb+ NaCl+ NH_4NO_3)

3.1.3 Root tissue of 7-day-old seedlings under stress conditions without Cad

A total of 12 bands appeared in control tissues of seedling roots, out of which peptides of molecular weight 56, 36, 34, 22, 20, 13.4 and 12.5 kDa were expressed remarkably (Figure 3). Some peptides were suppressed completely, namely at 44 and 40 kDa, or slightly at 56, 36, 34 kDa, or showed elevated expression at 12 kDa, under saline conditions. Also, the expression of peptides at 56, 44, 40, 36, 34, 22, 20, 13.4 kDa was affected in the presence of NH_4NO_3.

The non-expression of 44, 40 and 13.4 kDa in the root tissue with NH_4NO_3 over control seedlings was

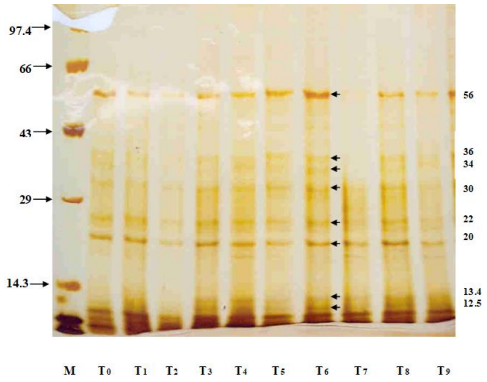

Figure 3. Protein profile of root tissue of 7-day-old seedlings under various stress conditions without Cad (M-Marker, T_0- Control, T_1- NaCl (100mM), T_2- NH_4NO_3, T_3- NaCl+ NH_4NO_3, T_4- Cd (1mM), T_5- Pb (1 mM), T_6- Cd+ NaCl, T_7- Pb+ NaCl, T_8- Cd+ NaCl+ NH_4NO_3, T_9- Pb+ NaCl+ NH_4NO_3)

intriguing. The peptides at 36, 34, 13.4 and 12.5 kDa got suppressed in NaCl+ NH_4NO_3 environment. Similar response was observed in the expression of peptides in Cd and Pb stress conditions. However, expression of peptides at 44, 30 kDa got suppressed by Cd but a novel peptide of molecular weight 18 kDa was induced. The expression of peptide at 40 kDa was found to be completely suppressed.

The peptide at 56 kDa got overexpressed along with the induction of a novel protein of 50 kDa under Cd+ NaCl stress conditions, while in the case of Pb+ NaCl environment the peptides at 56, 44, 36, 34, 30 kDa were suppressed completely, and the peptides at 22, 20, 13.4, 12.5 and 12 kDa were expressed a little. Inclusion of NH_4NO_3 to metal+ NaCl environment for the seedlings showed almost similar response to only metal in saline (metal+ NaCl).

3.1.4 Root tissue of 7-day-old seedlings under stress conditions with cad

Expression of proteins changed upon Cad enrichment in the plants that were in a stress environment (Figure 4). The expression of peptides at 70, 68, 49, 44, 36, 32, 30, 26, 22,18,16.8 and 14 kDa was induced by Cad, and their expression did not change when NaCl was added to the seedlings. However, slight suppression was observed for the peptides at 32 and 30 kDa under Cad+NaCl condition (T_1).

Also, protein expression induced by Cad did not alter upon NH_4NO_3 supplementation to those seedlings, but the expression of peptide at 84 kDa was observed. Interestingly, few variations were observed due to Cad in the presence of metals Cd and Pb. Change in protein bands were observed under metal+NaCl+NH_4NO_3 environment, such that depended upon the type of metal (Pb or Cd) used along with Cad.

3.2 Densitometric analysis of protein bands of leaf and root tissues

In order to have quantitative data on the proteins (which changed with treatments identified on SDS-PAGE), to identify differential expression of proteins and to remove

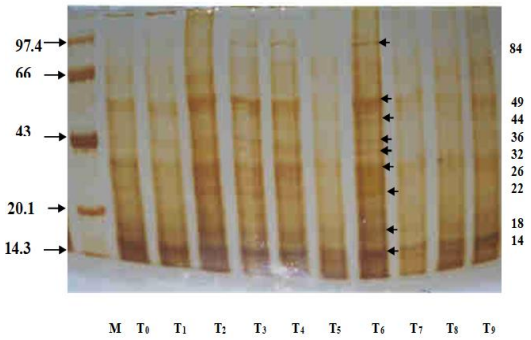

Figure 4. Protein profile of root tissue of 7-day-old seedlings under various stress conditions with Cad (M-Marker, T_0- Control, T_1- NaCl (100mM), T_2- NH_4NO_3, T_3- NaCl+ NH_4NO_3, T_4- Cd (1mM), T_5- Pb (1 mM), T_6- Cd+ NaCl, T_7- Pb+ NaCl, T_8- Cd+ NaCl+ NH_4NO_3, T_9- Pb+ NaCl+ NH_4NO_3)

results lacking significance, densitometry was done. This revealed some specific bands that have a high density in Cad treated tissues. Different peaks in the densitogram confirm the increased/decreased intensities of the bands (Tables 1, 2, 3, and 4; and Figures 5, 6, 7, and 8).

The leaves of seedlings without Cad exhibited 66, 56, 40.6, 35 and 22 kDa protein peaks in the densitogram. According to the peak area of protein band, the 66 kDa peptide had maximal expression with NH_4NO_3 and even in multiple stress conditions. The 56 kDa peptide had maximal expression with NH_4NO_3 and minimal in NaCl stressed leaf. Most strikingly the 22 kDa protein, as discussed earlier considered to be a member of protease family (Downing *et al.*, 1992), showed increased level in non-Cad treated leaves and its level decreased significantly with Cad. In the Cad treated leaf the 60, 56, 46, 39, 26 and 22 kDa proteins showed clear peaks in the densitogram indicating specific modulation.

Table 1. Densitogram data from SDS-PAGE gel, on proteins of leaf tissue in control and treated samples without Cad (areal percentages)

M.W.	T_0	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9
97.4	-	-	-	-	-	-	-	-	-	-
90	-	-	2415	-	3298	3839	3060	-	-	-
88	-	-	945	-	748	1760	1836	2052	980	1320
85	-	-	805	-	-	1800	1224	1548	-	-
80	-	-	1260	-	2142	3160	36	1188	280	1200
75	-	-	910	-	306	1240	1692	1332	525	440
66	210	280	2000	476	756	3185	385	180	2000	2030
56	740	1920	8050	1632	1728	1632	1152	952	1000	1280
51.8	-	1880	2765	735	-	4352	5328	468	1440	1440
50	-	520	-	-	1632	1085	108	1224	4520	4520
48	-	-	1085	2170	-	-	-	36	1200	1200
44	-	-	245	210	-	245	36	-	-	-
43	-	-	-	-	-	-	-	-	-	-
40.6	4352	540	920	805	805	920	630	-	-	-
37	1560	-	2310	445	1085	2310	36	-	-	-
35	-	-	2310	885	1120	1885	245	-	885	885
29.6	480	3080	558	-	-	558	-	-	-	-
29	-	-	-	-	-	-	-	-	-	-
24.6	440	720	4720	4410	805	4720	4720	5400	2080	2080
22	280	245	885	380	2310	805	480	-	-	280
20.1	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	2310	-
14.3	-	-	-	-	-	-	-	-	-	-
14	1520	-	1520	2310	2310	1520	1520	1520	885	2310
12	1360	-	1360	885	685	660	360	1360	558	885
11	4520	-	4520	558	558	4520	4520	4520	-	558

M.W. -Molecular weight, T_0- Control, T_1- NaCl (100mM), T_2- NH_4NO_3, T_3- NaCl+ NH_4NO_3, T_4- Cd (1mM), T_5- Pb (1 mM), T_6- Cd+ NaCl, T_7- Pb+ NaCl, T_8- Cd+ NaCl+ NH_4NO_3, T_9- Pb+ NaCl+ NH_4NO_3

Table 2. Densitogram data from SDS-PAGE gel, on proteins of leaf tissue in control and treated samples with Cad (areal percentages)

M.W.	T_0	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9
97.4	-	-	-	-	-	-	-	-	-	-
90	-	-	2415	-	3298	3839	3060	-	-	-
88	-	-	945	-	748	1760	1836	2052	980	1320
85	-	-	805	-	-	1800	1224	1548	-	-
80	-	-	1260	-	2142	3160	36	1188	280	1200
75	-	-	910	-	306	1240	1692	1332	525	440
66	210	280	2000	476	756	3185	385	180	2000	2030

Table 2. Continued

M.W.	T_0	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9
56	740	1920	8050	1632	1728	1632	1152	952	1000	1280
51.8	-	1880	2765	735	-	4352	5328	468	1440	1440
50	-	520	-	-	1632	1085	108	1224	4520	4520
48	-	-	1085	2170	-	-	-	36	1200	1200
44	-	-	245	210	-	245	36	-	-	-
43	-	-	-	-	-	-	-	-	-	-
40.6	4352	540	920	805	805	920	630	-	-	-
37	1560	-	2310	445	1085	2310	36	-	-	-
35	-	-	2310	885	1120	1885	245	-	885	885
29.6	480	3080	558	-	-	558	-	-	-	-
29	-	-	-	-	-	-	-	-	-	-
24.6	440	720	4720	4410	805	4720	4720	5400	2080	2080
22	280	245	885	380	2310	805	480	-	-	280
20.1	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	2310	-
14.3	-	-	-	-	-	-	-	-	-	-
14	1520	-	1520	2310	2310	1520	1520	1520	885	2310
12	1360	-	1360	885	685	660	360	1360	558	885
11	4520	-	4520	558	558	4520	4520	4520	-	558

M.W. -Molecular weight, T_0- Control, T_1- NaCl (100mM), T_2- NH_4NO_3, T_3- NaCl+ NH_4NO_3, T_4- Cd (1mM), T_5- Pb (1 mM), T_6- Cd+ NaCl, T_7- Pb+ NaCl, T_8- Cd+ NaCl+ NH_4NO_3, T_9- Pb+ NaCl+ NH_4NO_3

Table 3. Densitogram data from SDS-PAGE gel, on proteins of root tissue in control and treated samples without Cad (areal percentages)

M.W.	T_0	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9
56	390	117	117	117	840	42	835	-	939	539
50	-	-	-	-	-	-	140	-	-	-
44	780	-	-	4719	-	1248	420	-	160	3315
40	3003	-	-	-	6825	-	1400	-	4200	1755
36	234	320	482	925	950	1224	1053	-	209	352
34	1677	3510	429	1716	156	39	4934	-	760	1326
30	546	546	109	312	-	560	351	-	288	104
28	78	-	-	-	-	-	-	-	720	507
23	351	429	429	3120	663	1601	178	178	400	35
22	200	259	39	118	265	390	76	78	288	78
20	560	560	187	390	819	209	429	429	429	420
18	-	-	-	-	468	-	39	156	39	39
13.4	351	167	-	-	351	167	351	167	351	265
12.5	351	351	351	-	351	351	351	1232	351	351
12	351	429	351	546	351	351	351	556	351	351

M.W. -Molecular weight, T_0- Control, T_1- NaCl (100mM), T_2- NH_4NO_3, T_3- NaCl+ NH_4NO_3, T_4- Cd (1mM), T_5- Pb (1 mM), T_6- Cd+ NaCl, T_7- Pb+ NaCl, T_8- Cd+ NaCl+ NH_4NO_3, T_9- Pb+ NaCl+ NH_4NO_3

Table 4. Densitogram data from SDS-PAGE gel, on proteins of root tissue in control and treated samples with Cad (areal percentages)

M.W.	T_0	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9
100.2	-	-	-	-	-	-	4120	-	-	-
90	-	-	-	-	-	-	1080	-	-	3816
84	-	-	655	596	492	-	240	-	-	188
70	616	3919	540	572	1936	-	440	-	9100	2700
68	44	1600	1215	1012	2948	-	320	-	735	1116
49	390	327	540	400	274	180	412	132	104	233
44	1056	3040	990	748	4048	154	520	-	-	-
43	-	-	-	-	-	-	-	-	-	3600
36	136	110	252	60	192	-	2520	-	-	-
32	2332	4800	855	748	855	-	3160	-	-	520
30	176	176	1260	1276	1305	-	1480	1080	440	2520
26	-	-	1800	1276	-	-	1760	-	-	3160
22	148	130	290	135	290	74	117	-	320	85

Table 4. Continued

M.W.	T_0	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9
19	-	-	90	-	-	-	-	-	-	-
18	244	144	351	144	305	52	90	240	400	315
14	1408	1428	1677	1056	1120	810	351	3360	520	90
13.5	-	-	351	351	45	-	351	-	-	-

M.W. -Molecular weight, T_0- Control, T_1- NaCl (100mM), T_2- NH_4NO_3, T_3- NaCl+ NH_4NO_3, T_4- Cd (1mM), T_5- Pb (1 mM), T_6- Cd+ NaCl, T_7- Pb+ NaCl, T_8- Cd+ NaCl+ NH_4NO_3, T_9- Pb+ NaCl+ NH_4NO_3

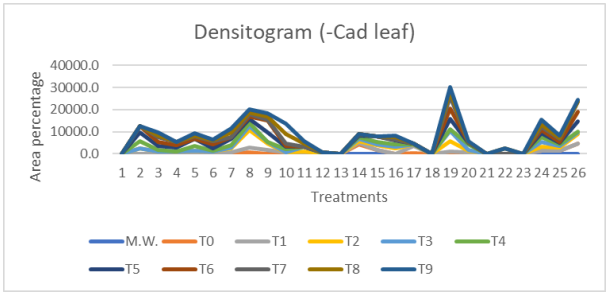

Figure 5. Densitometric spectra of the SDS-PAGE gel proteins from leaf tissue in control and treated samples without cad

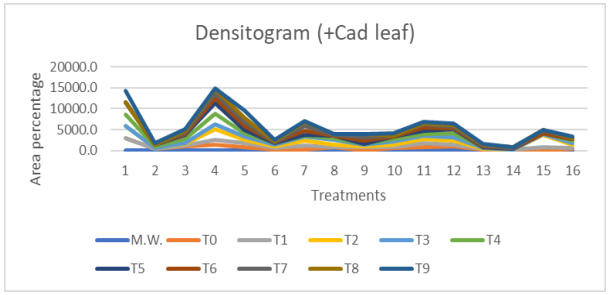

Figure 6. Densitometric spectra of the SDS-PAGE gel proteins from leaf tissue in control and treated samples with Cad

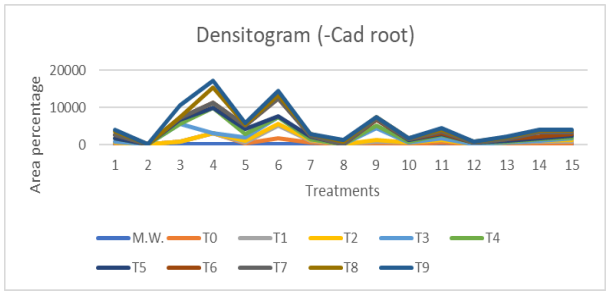

Figure 7. Densitometric spectra of the SDS-PAGE gel proteins from root tissue in control and treated samples without Cad

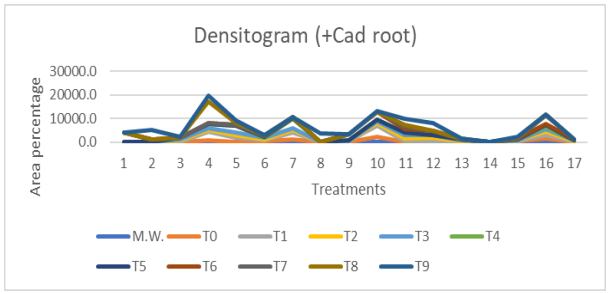

Figure 8. Densitometric spectra of the SDS-PAGE gel proteins from root tissue in control and treated samples with Cad

According to the band areas in non-Cad treated roots, the 56, 36, 30, 22 and 13.4 kDa peptides showed clear peaks and in Cad treated root the 84, 49, 36, 22 and 14 kDa pepides had high peaks (showed increased intensity). It is again worth mentioning that the 22 kDa peptide appeared to be common both in leaf and root with or without Cad. The 22 kDa peptide has been considered a protease in a number of studies (Downing *et al.*, 1992) and was very prominent in leaf and root tissues, otherwise increased by stresses and modulated by Cad. Several changes in proteins in B. napus leaf under water stress have been also noted (Reviron *et al.* 1992). Further experiments to determine the roles of Cad induced proteins are required.

4. Conclusions

In order to elaborate the mechanisms of stress tolerance in Brassica species in the presence of Cad, the protein profiles were determined. The SDS analysis revealed the appearance of several specific polypeptides. However, due to salt and metal stress peptides at 60, 56, 51.8 and 22 kDa were observed. Cad stimulated the synthesis of 46 and 14.9 kDa peptides in root tissue, whereas induction of 56, 36, 34, 23, 20, 13.4 and 12.5 kDa peptides with Cad were remarkable and concomitantly the 22 kDa peptide was suppressed. During stress, it is quite possible that the changes in peptide pattern due to salinity/metals may be involved in growth-related biochemical functions. Densitometric analysis supports the results of protein expression with treatment. The identification and characterization of some of the relevant proteins and their genes may provide some insights regarding the regulation mechanisms associated with salt stress, at the molecular level.

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