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„Subcellular Fractionation of Pisum Sativum“

verfasst von / submitted by

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Contents

List of abbreviations

NAF	Non-aqueous fractionation
Me	Mesire cultivar (Pisum sativum)
pr	Protecta cultivar (Pisum sativum)
LC-MS	Liquid chromatrography and Mass spectrometry
GC-MS	Gas chromatography and Mass spectrometry
NP	Plants fertilized with nitrogen and phosphorus
R	Plants inoculated with rhizobia
I	infected
h	healthy(not infected)
UZ	Ultra zentrifuge
NSAF	normalized spectral abundance factor
FA	formic acid
LC-MS	Liquid chromatrography – mass spectrometry
R gene	resistance gene

1. Abstract

The non-aqueous fractionation (NAF) was developed to particularly sub fractionate metabolites from plant material. Previously, NAF has already shown to allow for a concerted metabolite and protein analysis. The separation allows an increased resolution when identifying via Mass Spectrometry (MS). It enables the separation of subcellular organelles such as chloroplasts, cytoplasm and vacuole and their concomitant metabolites and proteins for localization.

In a pathogenic attack via *Didymella pinodes* plants such as *Pisum sativum* activate their immune system at different organelle levels to counteract the pathogen.
In my master thesis, I investigated the response to the pathogen on a subcellular protein level. Furthermore, I evaluated organelle marker proteins through multiple experiments.

2. Introduction

2.1 Non-aqueous fractionation

In opposite of the commonly used technique of a 2D gel electrophoresis and further analysis there is no amplification or purification step for proteins required in NAF. High abundant proteins such as RuBisCO (Ribulose-1,5-bisphosphat-carboxylase/-oxygenase) could conceal low abundant proteins if the complex cell lysate would be analyzed with a 2D gel electrophoresis unlike with the separation into multiple fraction via NAF and afterwards coupled to LC-MS. By doing so even small traces of proteins can be found despite the high abundance of RuBisCO. (Klose, 1975) (O'Farrell, 1975) Many regulatory proteins, which act like switches and are located in key positions of the metabolism, only exist in specific subcellular compartments and have a low number of copies and are not easily detectable by those techniques mentioned before. (Huber, Pfaller, & Vietor, 2003) To determine the exact subcellular locations and concentrations of proteins and metabolites in a eukaryotic cell NAF is required. In aquatic-environments such as sucrose-gradients metabolites unlike proteins have rapid turnover rates, as low as 1 second.(Arrivault et al., 2009) To conserve the metabolites *in vivo* a waterless gradient need to be used.

Furthermore for identifying the subcellular location of proteins and metabolites as well as of those proteins with low abundances, organelles need to be isolated in high purity and this is achieved by the partial analysis of the density gradient.(Arrivault et al., 2014) For this purpose multiple fractions need to be taken off top-down from the density gradient and analyzed via "shotgun" approach.

The key of the non-aqueous fractionation lies within the density gradient since this gradient separates the proteins based on their molecular weight. At specific densities, certain subcellular organelles and their associated proteins are captured, e.g. vacuole associated proteins have the highest molecular weight and are found almost unexceptional at the very bottom of the gradient since they are able to pass even high densities in contrast to chloroplast associated proteins. Most of them are collected near the top of the gradient, because of their lower molecular weight and thus in the first fractions.

2.2 Proteomics and Mass Spectrometry

Proteomics is the large-scale study of proteins. (Anderson & Anderson, 1998) The Proteome describes the complete set of proteins of an organism, although the size can vary depending on e.g. environmental influences or other distinct influences such as stress and time. The investigation on such fluctuation, either of just single proteins which are located in key position of the metabolism and control specific responses to environmental changes, or larger groups of related proteins which may vary in number of copies or location.

In recent years the number of identified proteins specific for a cellular compartment has increased simply because of the improvements of mass-spectrometry techniques coupled to proteomic methods. This way it has become possible to characterize complete proteomes among others from human centrosome and Arabidopsis. (Andersen et al., 2003; Dunkley et al., 2006; Dunkley, Watson, Griffin, Dupree, & Lilley, 2004; Nikolovski et al., 2012)

The importance of those fast screening methods lies in the vast amount of proteins which are expressed by a genome or cell under defined conditions. The proteomes of eukaryotes are in large parts bigger than the genome due to alternative splicing and post-translational modifications, therefor 5 to 10 different protein variations can be produced from one gene. Another level of complexity is added due to the varying range of different protein expression levels in a cell, this can range from 10^6 to 10^9 copies per cell. (Frohlich & Arnold, 2006)

To sustain a sensitive and selective analysis for complex compound mixtures, while relying on high-throughput analysis of proteins, is one of the biggest challenges in today's Proteomics. (Klie et al., 2011) MS has become the analytical tool with high-throughput capacities coupled to sensitive separation techniques which preserve the complex information. (Griffin, Goodlett, & Aebersold, 2001)

The detection of proteins are achieved by cleaving proteins into peptides and identify them by mass fingerprinting. The identity of the protein is achieved by matching the observed peptide mass against a sequence database. The tandem mass spectrometry can get the sequence information of the peptide by colliding the peptide with a non-reactive gas and identifying the generated ion fragments. (Altelaar, Munoz, & Heck, 2013; Wilhelm et al., 2014)

Two ionization techniques have become apparent, ESI (electrospray ionization) and MALDI(Matrix-assisted lase desorption/ionization). However, only ESI was used due to its better applicability because ESI MS can produce highly charged ions directly from liquids unlike MALDI where samples are fixated to a solid matrix. (Domon & Aebersold, 2006; Fenn, Mann, Meng, Wong, & Whitehouse, 1989)

2.3 Liquid chromatography mass spectrometry

LC-MS/MS

Before the analyzation via mass spectrometry the sample mixture undergoes a separation based on the level of interaction of the molecules with the adsorbent e.g. C18(octadecylsilyl) with a pore size of 30nm. The C18-granula serves as the stationary phase while the mobile phase, mostly a pressurized (up to 350bar) liquid consisting of various solvents such as water, acetonitrile and methanol slowly elutes the molecules which are bound to the adsorbent by taking its place. By gradually increasing the eluting strength of the liquid phase the sample mixture gets separated and generates a unique retention time(RT) for each molecule. After the eluting via the use of the HPLC (high performance liquid chromatography)(Brown, 1970) the analytical chemistry technique of mass spectrometry measures the mass-to-charge ratio of the charged molecules and is mainly used for the identification of molecules in a sample by determining the elemental composition as well as the identification of the molecular structure of molecules such as proteins.(Wysocki, Resing, Zhang, & Cheng, 2005) To measure a sample, it is vaporized via electrospray ionization (ESI) and molecules are ionized . By using the ESI, multiple charged ions are generated and increase the effective mass range for the analyzer. Another advantage is the lower fragmentation rate and so the precursor ions are more accurately observed. The so scanned precursor ion is specifically fragmented via collision induced dissociation(CID) and then scanned in the second mass analyzer.(Wells & McLuckey, 2005) The CID technique fragments molecular ions via energizing those ions and letting them collide with neutral molecules(no charge) such as argon. By this collision some of the kinetic energy is transformed into internal energy and by doing so the molecules are fragmented via breaking some of the molecular bonds. The smaller fragments now can be analyzed, in this experiments via an orbitrap. The ions pass via the C-trap into the orbitrap where the ions are trapped and cycle around the inner electrode in an elliptical orbit. The axial oscillation of the ions is detected and converted to a mass spectrum based on their mass to charge ratio (m/z) via Fourier transformation. (Olsen et al., 2007)

2.4 Pea cultivars

As plant material *Pisum sativum* was used, which is better known as common pea with its characterizing spherical seeds which it has in common with every other plant of the Fabaceae family. With a life cycle of just one year *Pisum sativum* is an annual plant with the major benefit of being a crop, able to also grow in the cooler seasons of the year. The origins of *Pisum sativum* lies in the Near East up to Greece and dates back 4800BC but isn't restricted to this areas nowadays.(Helback, 1959)

2.5 Compartments

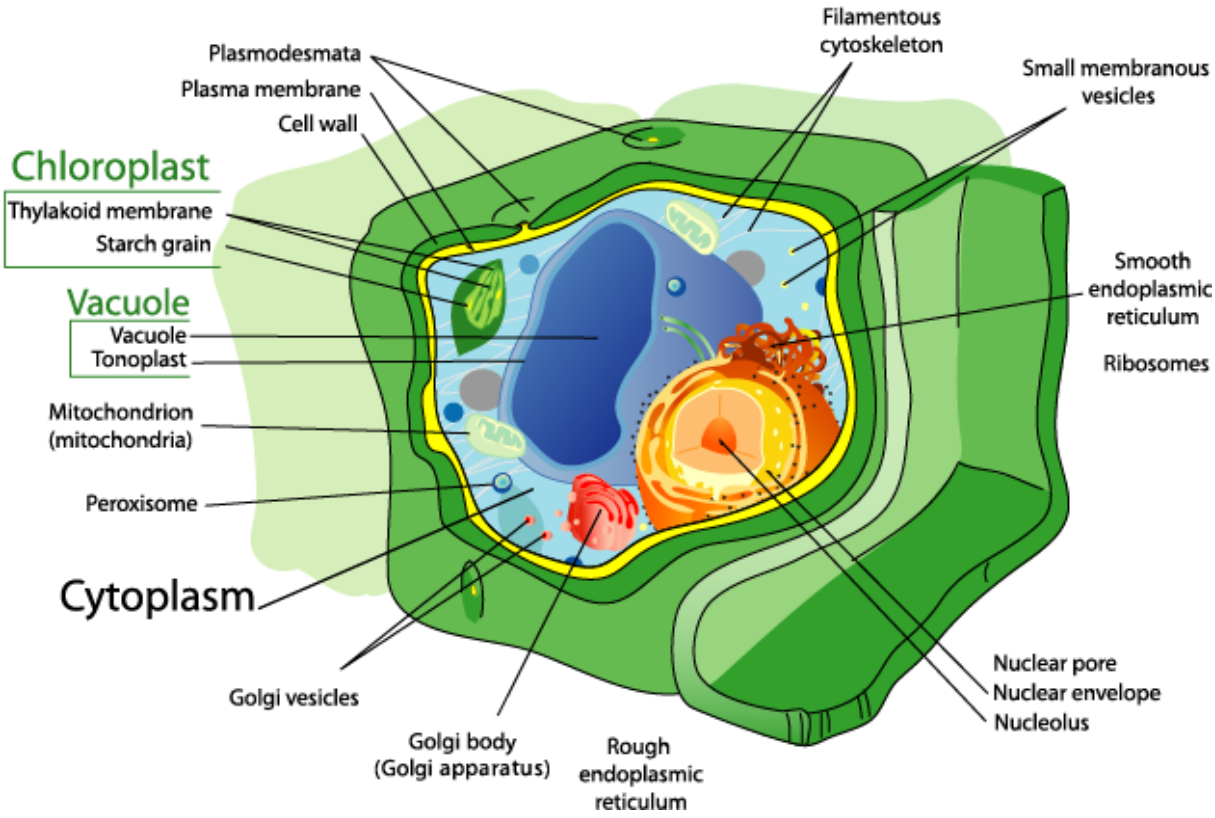


Fig. 1. The plant cell consists of multiple subcellular organelles, main focus lied on the chloroplasts, vacuole and cytoplasm, although the cytoplasm serves as a collecting point. (Villarreal, 2006)

2.6 Plant-pathogen interaction

Plants have developed a strongly distinctive immune system compared to non-stationary eukaryotes, to defend them against pathogens when they penetrate the cell walls, their first layer of defense. (Dangl, Horvath, & Staskawicz, 2013) The immune system of plants is based on the ability of transferring defensive molecules via the vascular system to every cell to activate their defense systems. (Dadakova et al., 2015) The plant immune system relies on two interconnected receptors to detect foreign molecules. Pathogen associated molecular patterns(PAMPs) are used to trigger an intracellular response to limit the pathogenic attack. (Jones & Dangl, 2006)

As a second defense mechanism R genes and their products are used to reveal specific pathogen effectors and trigger a customized response against the pathogene. (Nurnberger, Brunner, Kemmerling, & Piater, 2004) *Didymela pinodes* is a major and highly specific pathogen for Pisum sativum.

2.7 Aims of this work

Non-aqueous fractionation was used to gain insight and knowledge about the subcellular proteome pattern of the different organelles in leaf tissue of two different Pea cultivars (Messire and Protecta) in response to pathogenic attack.

In order to achieve reproducible results the technique of NAF had to be established for Pea. I evaluated the various NAF gradients for reproducibility and efficiency in terms of subcellular resolving power. Therefore, subcellular standard peptides were determined.

3. Materials and Methods

Plant Material

For this thesis two different cultivars of *Pisum sativum*, Protecta and Messire were used and observed regarding the differences in their response to pathogenic stress. Messire it is known to be more susceptible to D. pinodes than Protecta. (Murray, 2011)

The other plant used for Experiment was *Arabidopis thaliana*, more precisely the Columbia cultivar. The leaf material for A. *thaliana* was thankfully provided by Thomas Nägele.

The harvested leaf material, from *P. Sativum* as well as from *A. thaliana* was frozen as quickly as possible in an aluminum bag after the harvest in liquid nitrogen to stop the metabolism. The frozen leaves were stored at -80°C before grinding to a homogenized powder in a mortar which had been precooled with liquid nitrogen to prevent the sample from unfreezing. 150mg of leaf powder was put in a precooled 50ml glass flask and then attached to an also precooled lyophile for freeze-drying at -18°C and 4Pa for 72h. Freeze-dried material was stored at -80°C until further use.

3.1 Non-aqueous fractionation

For pouring the density gradient (5 ml C_2CL_4/C_7H_{16} and 5 ml C_2CL_4) a BioRad EP-1 Econo peristaltic pump was used to pour a 9ml density gradient into a tube with a max. volume of 10 ml. To maintain the exact amount of organic solvent for each gradient a hose was used, which could withstand the organic solvent and also the mechanic pressure of the peristaltic pump which tended to prolong the hose and thus change the volume of it.

The density of C_2CL_4/C_7H_{16} with v/v = 70:30 is d=1,34 g/cm^3 and the density of C_2CL_4 is d=1,625g/cm^3 therefore the gradient was poured, so the density decreases the from the bottom to the top.

The pouring time is 11:23min per gradient with a dead volume of 2:23min and a pump rate of 1ml/min. Therefore the final gradient was 9ml.

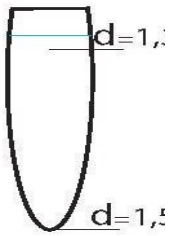


Fig. 2. Example of decreasing density of the gradient

At the surface of the density gradient the density is 1,34 g/cm^3 and slowly decreases to an approximate density of 1,54 g/cm^3.

To ensure a consistent gradient for every non-aqueous fractionation during the experiments more than 30 gradients were poured and checked for a steady distribution of the densities within the gradient. This was done by taking 9 fraction each 1ml from the surface to the bottom putting the mixture into preweighed 1,5ml Eppendorf tubes. By weighing them the density could be determined for each separately and therefore checked.
75mg of the lyophilized material were put into a glass jar tube and then 10ml of C_2CL_4/C_7H_{16} are added. To homogenize the resolved leaf material the jar is ultrasonicated in a ultrasonicate bath for 12min. To prevent the solvent from heating up, after 5sec of ultrasonicating the jar was put on ice for 20sec and then the process was repeated until 12min of ultrasonicating.
For filtration of bigger particles a myo cloth with a pore size of 30nm was used and poured into a 50ml falcon tube. The myo cloth was rinsed 2 times with 5ml ice-cold C_7H_{16}. The tube was centrifugated for 10mins at 4°C at 4500rpm and afterwards the supernatant is discarded and the pellet re-suspended with 1.5ml C_2CL_4/C_7H_{16} d=1,35.
1ml was loaded on top of the freshly poured density gradient and tared to an accuracy of 0.01g. The density gradient was then centrifugated for 3h at 4°C with 30.000g in an ultracentrifuge (Beckman instruments *SW4ITI* 6 bucket rotor). As soon as the ultracentrifuge stopped 9 fractions are collected top-down from the gradient into 2ml Eppis, each fraction á 1ml and stored on ice. The 1ml fractions were aliquoted into 3x300µl and diluted with 1ml C_7H_{16} and centrifugated for 3min at 4°C with 13.000rpm. 1ml of the supernatant was discarded and then dried in the speed-vac for 1.30h to completely dry. Subsequently the samples are stored at -80°C.

3.2 Preparation for protein analysis

3.2.1 Protein extraction

Urea buffer	
Hepes, pH 7.8	500 mM
Urea	8 M
Bradford solution	
ddH_2O	225 ml
Ethanol	15 ml
Phosphor acid 85%	30 ml
Coomassie brilliant blue g-250	150 mg

Protein extraction was performed by adding 300µl Urea-buffer (*9ml Urea 8M, 1ml HEPES(pH=7.8))* to the at -80°C frozen samples which were re-suspended in it, then put on ice for 10min. After centrifugation for 10min at 4°C with 10.000g 1.5ml Acetone with 0.5% 2-mercapthoethanol were added to reduce disulfide bonds and after a short time of vortexing the tubes are stored overnight at -20°C.

After a centrifugation with 3.500rpm for 15min at 4°C the supernatant was discarded and the pellet once again re-suspended with 1.5ml ice-cold methanol. The tube was centrifugated once again with 3.500rpm at 4°C and the supernatant is also discarded and the pellet is dried which is re-suspended in 50µl Urea-buffer. To determine the concentration of the protein a Bradford assay was performed as well as a BSA standard calibration curve. (Bradford, 1976; Staudinger et al., 2012)

3.2.2 Protein digestion

Proteins were digested in solution, therefore already diluted in the urea buffer. For every 100µg protein calculated via Bradford 1µl endoproteinase LsyC 200µg/ml was added for predigesting. Every sample was filled up to 100µl with ureabuffer and digested for 5:30h at 30°C in a Thermo shaker covered with tinfoil due to the light sensitivity of LysC. The sample was again diluted with a 3-fold Trypsin buffer(300µL) and then 3,3µL Trypsin were added for every 100µg protein for digestion over night at 37°C in a hybridization oven. The reaction was stopped by putting the samples on ice for 5min. (Staudinger et al., 2012)

Trypsin buffer	
H2O	79%
ACN	10%
Ammonium bicarbonate	100 mM CaCl2
Dithiothreitol	5 mM

LysC is an endoproteinase which cleaved on the c-terminal site of lysine and the reason for this predigesting was, that LysC has a higher specificity then Trypsin for cleaving lysine. Trypsin, which cleaved on the c-terminal site of arginine and lysine, didn't need much time to completely digest the remaining cleavage sites. If only cleaved by Trypsin, it would take much longer and by that, the risk of miss cleaving could increase.

3.2.3 Desalting

The desalting step was performed via C18 stage tips (Rappsilber, Ishihama, & Mann, 2003) by equilibrating the membrane once with 100µl MeOH and 0,l%FA(formic acid) and then 2 times with 100µl ddH_2O with 0,l%FA. The samples were spun down at 4°C to get rid of the Trypsin. Carefully the supernatant was taken off and pipetted in the C18 stage tip. The sample was pipetted multiple times through the tip to make sure the peptides had bound before washing them 2 times with ddH_2O with 0,l%FA. The bound peptides were then eluted into 0,5ml low-bind eppis with two times 100µl MeOH with 0,l%FA and dried down in the speed-vac and afterwards stored at -20°C. (Rappsilber et al., 2003)

3.2.4 LC-MS/MS based analyzation

The peptides of each sample were dissolved in 25µl 2%ACN, 0.1%FA and applied on a reverse phase C18 2µm analytical column (Thermo Fisher scientific) and the peptides were eluted with a linear gradient of 5% to 95% Acetonitril over 90 minutes with a flowrate of 250nL min^{-1}. Peptides were analyzed on a LTQ Orbitrap Elite (Thermo Fisher scientific).

3.3 Protein Identification

For identification, a custom database was used which was made available by Reinhard Turetschek containing the *P. sativum*, *R. leguminosarum*, *Glomus* and *Mycosphaerella* protein dataset which also included known contaminants such as human keratin, trypsin from digestion etc.

For identification of the raw files MaxQuant version 1.5.3.30 (Cox & Mann, 2008) was used. Furthermore, the oxidation of methionine was set as a fixed modification and up to 2 missed cleavages were allowed. The mass tolerance was set at 10ppm for full scans and 0.5 Da for fragmented ions. The retention time window was set to 2mins.
Following parameters were used to quantify the datasets:
Digestion for Trypsin/P and Lysion/P, Modifications Oxidation (M) and Acetyl (Proteins-N-term), Label-free quantification (LFQ), Instrument Type Orbitrap with 20 peptide tolerance for first search, 4.5 peptide tolerance for main search. Peak min. length was set to 2 with max. charge 7. For fixed modification Carbamidomethyl(C) was set, Sequence length was set to min. peptide length of 7 and max. peptide mass to 4600kDa.
For Protein quantification the min. ratio count was set to 2 and was done via Unique + razor.

4. Results

4.1 Non-aqueous fractionation

The typical gradient was split into 9 fractions (p1-p9) each 1ml. As one aim of this work was, to ensure stable gradients. The focus lied on increasing the chance of identifying the three subcellular compartments such as plastid, cytosol and vacuole.

At the top the dark green phases, p1 and p2 have high abundances in plastid-proteins and intentionally RuBisCO related proteins weren't chosen as a peptid marker, because of the high abundance and therefore higher risk of smearing and lack of accuracy when annotating to a subcellular localization. The cytosol associated proteins were found through phase p3-p8 and yielded to most proteins combined with the highest range of variation. The dominant proteins in p9 were, as expected, vacuolar proteins and were the most stable regarding the repeatability of the detection.

Marker peptides identifications were used to assess whether the NAF worked or not, due to the complexity and steps to prepare the samples.

Fig. 3. The NAF gradient shortly after ultracentrifugation before splitting it into 9 fractions. The change in color, from dark green where the chloroplast associated proteins are to light green where most of the cytosolic proteins are up to the transparent fraction where the density is the highest with about 1,55g/cm^3 and the vacuolar proteins are located.

Total performed NAFs

In total 36 non-aqueous fractionations were performed during this master thesis with a reproducibility rate of approximately 70% .

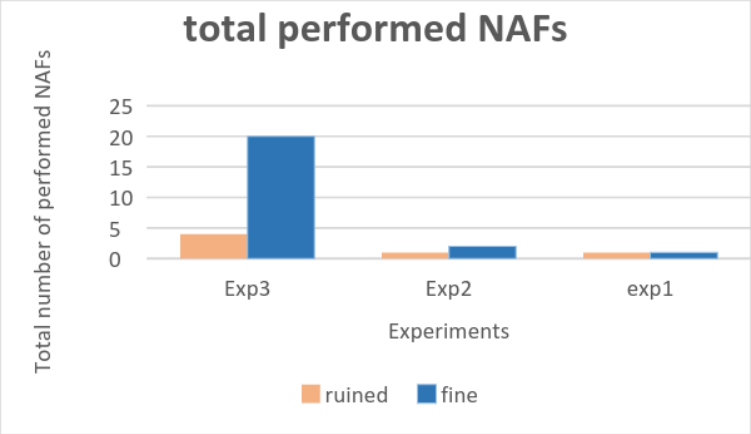


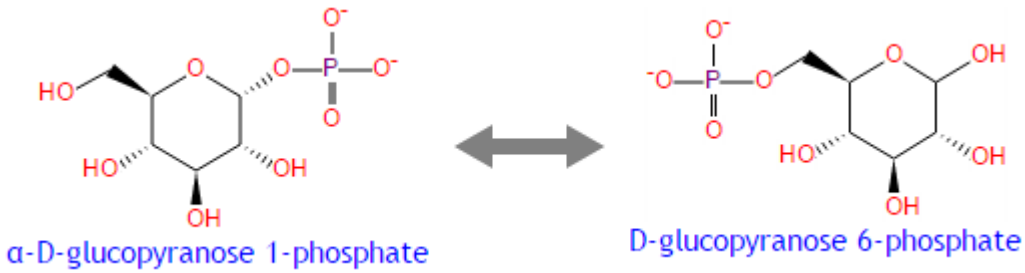
Fig. 4. The reproducibility rate of gradients was increased during the master thesis, due to adapting existing protocols for Arabidopsis to the *Pisum sativum*.

Used marker peptides:

To identify marker peptides for *P. sativum* marker peptides already found for *A. thaliana* were used as a reference in the first experiment. This was done to evaluate the distribution of the proteins. Further three different marker proteins were identified for *P. sativum* and used for evaluation of the gradients.

Chloroplast	Phosphoglucomutase
Cytoplasma	UDP-glucose 6-dehydrogenase
Vacuole	Bifunctional purple acid phosphatase 26

Fig. 5. **h o s p h o**



glucomutase plays a major role in the glycogenolysis by easing the interconversion of glucose-1-phosphate and glucose-6-phosphate by transferring the phosphate group from the 1’ to the 6’ postion of an alpha-D-glucose. (Caspi et al., 2014; Sutherland, Cohn, & et al., 1949

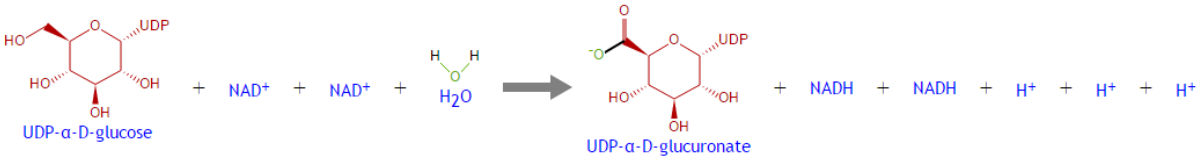


Fig. 6. **UDP-glucose 6-dehydrogenase** is a confirmed cytosolic protein and plays a major role in 4 metabolic pathways, such as the starch metabolism. (Caspi et al., 2014; Spicer, Kaback, Smith, & Seldin, 1998)

Bifunctional purple acid phosphatase 26 is an annotaed metallo-phosphoesterase and mostly involved in the phosphate metabolism and primarily picked as a marker protein because of its high abundance in the vacuole fractions.(Bozzo, Raghothama, & Plaxton, 2004)

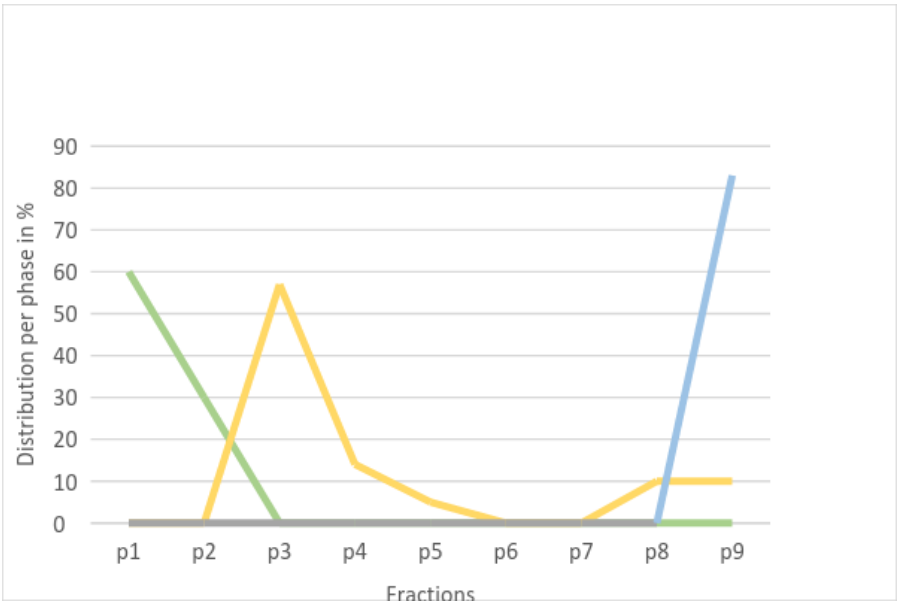


Fig. 7. Marker proteins for evaluating gradients.

The phosphoglucomutase showed a reproducible abundance in the chloroplastical phases. Also the UDP-glucose 6-dehydrogenase was reproducible found in the cytosol phase as well as in the vacuole phase, most likely due to the centrifugation, since at the end of the flask, traces of all proteins were collected in difference abundance. For the vacuole marker Bifunctional purple acid phosphatase 26 was chosen, because of the high abundance in the p8 and p9 phases of the gradient.

4.2 Protein distribution in the gradient in terms of relative quantity

Each fraction not only showed different abundances of proteins, but also the absolute quantity of proteins in each fraction differed.

4.3 Proteomic NAF analysis

4.3.1 Experiment **1**

The first experiment was done with a leaf sample of a single *Pisum sativum* plant to evaluate the challenges of the NAF. In the first NAF attempt 760 proteins had been identified, although only one of two gradients could be analyzed. As a first result the relative distribution of protein levels over each fraction were analyzed.

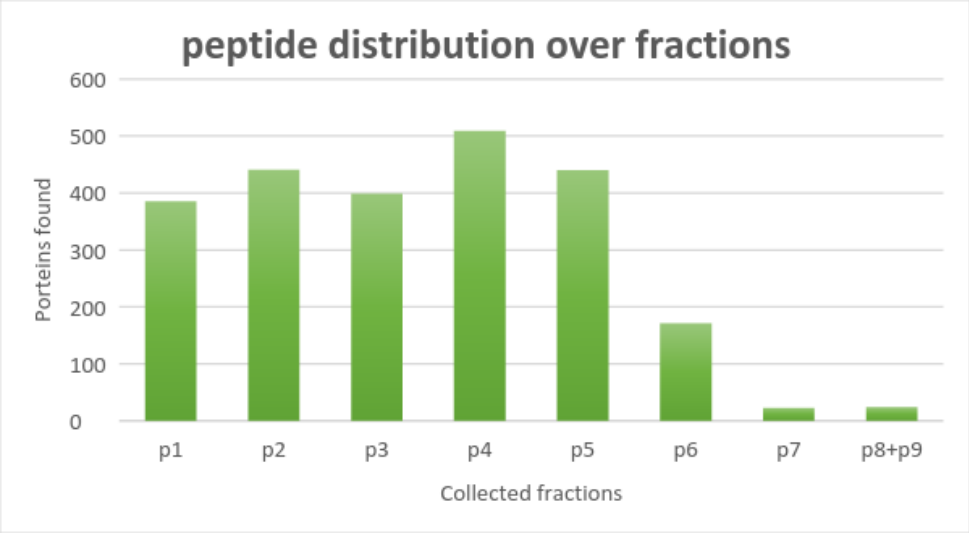


Fig. 8. Absolute number of identified peptides found in gradient from control sample of cv. Messire.

The distribution in Fig.7 doesn't show the relative abundance of peptides, but the amount of peptides found per fraction. Also, peptides were counted as unique for each fraction, even if they were found in different fractions multiple times.
It is clearly visible that the lower fractions, especially fraction 7, 8 and 9 are relatively empty compared to the other fractions. The last two fractions had to be pooled together to even reach a detectable amount of protein level.

4.3.2 Experiment **2**

The second experiment was done by analyzing 3 leaf samples of *Pisum sativum* provided by Reinhart Turetschek. The samples were extracted at 2 different times and had also been analyzed twice to increase the reliability of each sample. Thus, altogether 6 gradients were performed. Unfortunately, one gradient had to be discarded leaving 5 complete gradients for evaluation with regards to reproducibility and accuracy. A total of 1047 different proteins were identified in the 9 fractions from the remaining 5 analyzed gradients.

The spectral count was used with normalized spectral abundance factor to normalize the abundance of each protein. All proteins were split into chloroplastic/cytosolic/vacuolic affiliation, by their behavior compared to the marker proteins as well as subcellular prediction (Horton et al., 2007). and then plotted. The average of the peptide count for every specific subcellular compartment was plotted and as well used to proof if the NAF had worked out.

In the 2. Experiment the focus lied on the behavior of the individual proteins, questioning the separation of the compartments as well as single proteins, as expected in the last and 3. Experiment. The main focus changed to the general clustering of the analyzed fractions, assuming every gradient behaved in a similar way as the gradients did in the 2nd experiment.

Chloroplastic:

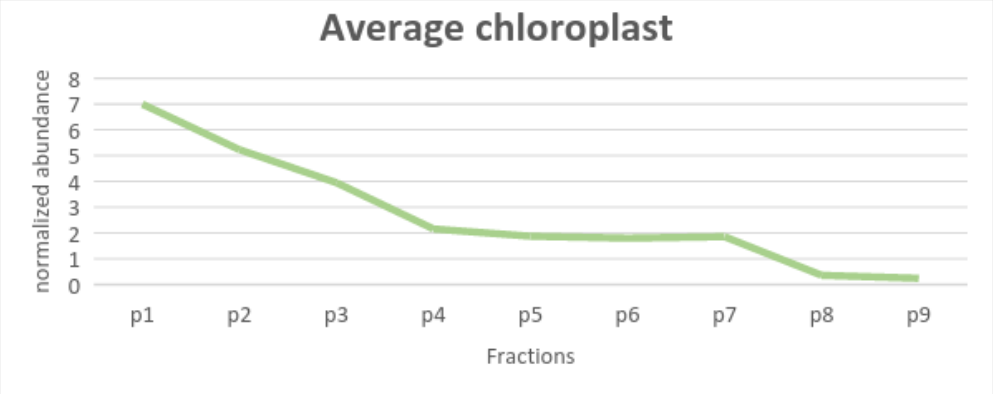


Fig. 9. In total 184 proteins were identified as chloroplastic.

Not every chloroplastic protein was found exclusively in the p1 and p2 fraction of the gradient, some tended to smear through the gradient and were found in a low abundance through all fractions of the gradient.

Cytosolic proteins:

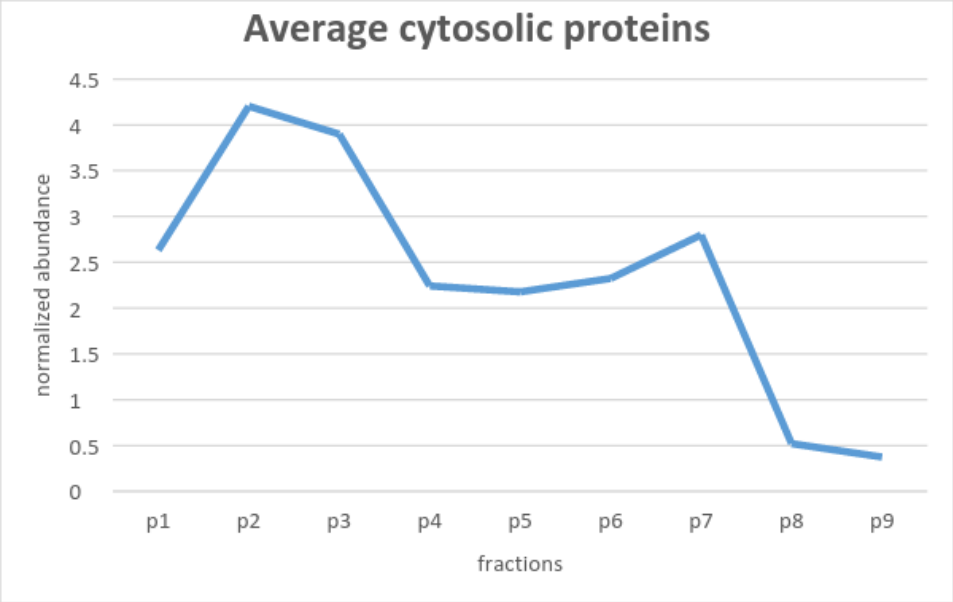


Fig. 10. In total 84 proteins were identified as cytosolic.

Cytosolic proteins tended to smear through the whole gradient with two abundant peaks in p2 and p7, but this smearing from p2 to p7 is not untypical and also found for marker peptides sometimes.

Vacuole proteins:

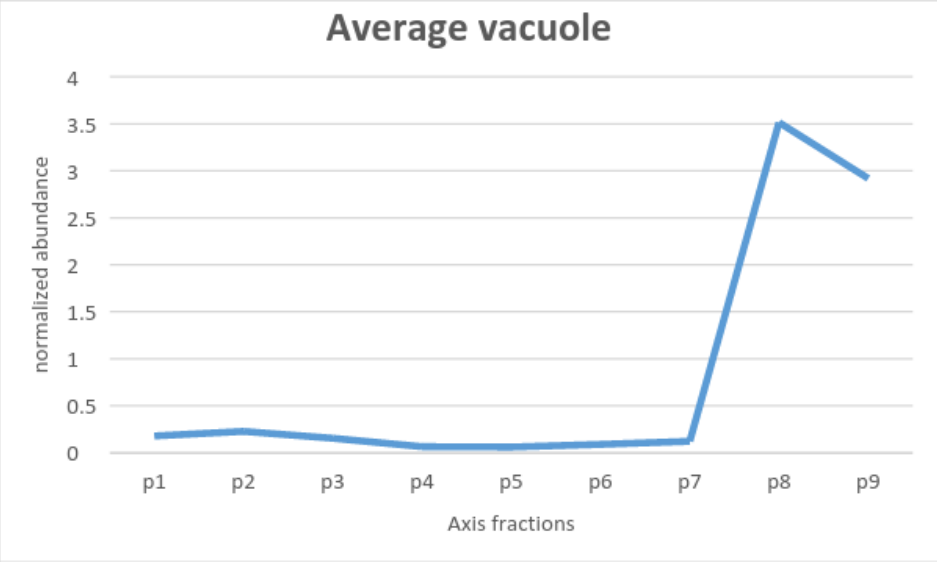


Fig. 11. In total 83 proteins were identified as vacuolar.

The vacuole proteins gathered up in the last two phase p8 and p9 as expected due to the high mass of this proteins.

The second Experiment showed that the separation of the three subcellular compartments was reproducible. The abundance of chloroplastic proteins were decreasing though the fractions and is mainly found in p1-p4 although traces of some chloroplastic proteins could be found till p7. The cytosolic compartment had spread from p3 to p7, although the fact that they were found even in those fractions(p1+p2) which only should have contained chloroplastic proteins. That indicated some problems with the gradient at the highest fractions, in which the gradient had the lowest density. In p8 and p9 almost exclusively vacuolar proteins could be identified, which proofed that the lower fraction in the density gradient had worked as intended.

Only 351 proteins could be identified as *Pisum sativum* proteins and specifically matched to a subcellular compartment such as chloroplasts/cytosol/vacuole. 703 proteins remained unspecific or not clearly identified. The identification of *Pisum sativum* proteins were likely more inaccurate due to incomplete proteome databases. The used databases are a combination of confirmed *Pisum sativum* proteins and the *Medicago truncatula* proteome. The remaining 703 proteins could only be clustered to the most likely compartment due to their behavior in the gradient.

4.3.3 Experiment 3

For the 3. Experiment the leaf material of *Pisum sativum* was once again provided by Reinhart Turetschek. The leaf material was divided into non-infected (healthy) and normally nutritioned Messire and Protecta cultivars. The 2nd group was Rhizobia infected Messire and Protecta cultivars.

Every sample was then fractionized via NAF into 9 fractions, totaling at 216 fractions. A fast screening with the marker peptides from experiment 2 was done to validate the usability of each gradient, 3 gradients were ruled out due to clear misbehavior of the distribution. The presumption was, that those 3 gradients had been ruined during the NAF. The 3 ruined gradients were 5, 8 and 13. However there was still multiple replicants of the missing treatments remaining.

healthy	R-ME	R-Pr	NP-ME	R-ME	R-Pr	NP-Pr
sample#	5	8	13	16	30	36
	R-Me	R-Pr	NP-Pr	NP-Pr	NP-Me	NP-Me
	39	42	43	58	61	67
infected	NP-ME	NP-Me	NP-Pr	NP-Pr	R-Pr	R-Me
sample#	74	80	83	98	99	102
	NP-Pr	R-Pr	R-Me	NP-Me	R-Pr	R-Me
	105	111	125	128	133	136

Table. 1. **The 3rd Experiment** showed the different reactions to a pathogenic attack on the two cultivars Messire and Protecta. Two different nutrition's, fertilized with nitrogen and phosphorus or infected with mycorrhiza were used. For each treatment 3 replicates were used.

The *Pisum sativum* cultivars Messire and Protecta were grown in 2014 in a greenhouse in Tulln at the Department für Agrartechnologie Boku. Two different treatments were applied to an infected group as well as to an uninfected group. R for rhizobia and NP for nitrogen and phosphorus fertilization.
The infection of the *Pisum sativum* cultivars was done with *Didymella pinodes* which had been bred on petri dishes to guarantee enough spores for a successful infection. After 2 weeks of growing, the healthy control group was covered in order to not get infected. The infection was performed by covering the petri dish with the pathogen with 10ml of water to collect many of the fungus spores. This mixture was once filtered and diluted again with water and filled into spray bottles. The aerosol with the spores was applied onto the plants one time.

For the analyzation, the distribution of the proteins NSAF (normalized spectral abundance factor) was used as well as the normalized unique peptides relatively to the total abundance of them in each of the fractions. Although the following graphs only show the normalized values via the unique peptides.
2769 proteins were found in the combined 216 fraction in the 3. experiment and although not every protein was found in every gradient the majority was found in at least 1 other sample.

4.3.4 Analysis of the fractionation efficiency

In the following, the efficiency of the subcellular separation and validation of the subcellular location via marker proteins are shown.

4.3.4.1 Chloroplast fractions

The normalized LFQ intensities were analyzed by dividing the fraction intensity by the absolute intensity of the gradient. The average intensity through all fractions was plotted (in red) as well as the intensities of every single protein. As a marker protein for the chloroplast fractions Phosphoglucomutase was used again. Clearly visible is the decrease through the fraction. The highest abundance was measured in the first 2 fractions (p1+p2) as intended. The deviating lines showed the high range of variation.

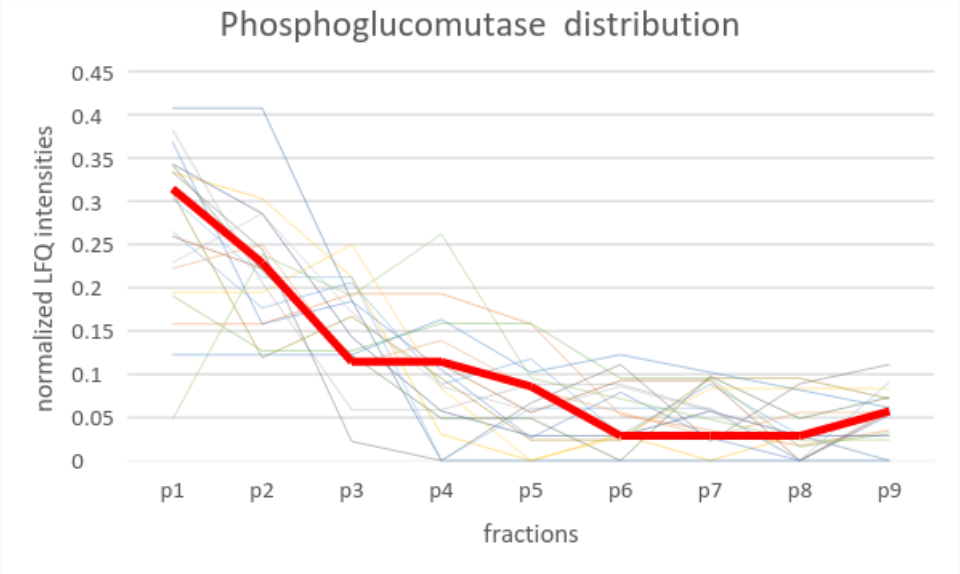


Fig. 12. **Phosphoglucomutase** showed a clear distributation in the first fraction, respectively p1 and p2. Phosphoglucomutase is predicted to be located in the chloroplast (n=20).

4.3.4.2 Cytoplasmatic fractions

UDP-glucose 6-dehydrogenase was used again as a marker protein to validate the distribution of the cytoplasmatic proteins through the gradient.

Although the distribution of UDP-glucose 6-dehydrogenase was not as clear as in experiment 2, the distribution of the cytosol was clearly visible from p2 to p7. Proteins related to the cytoplasm were difficult to locate because of their natural behavior in the cells. This behavior of being everywhere is shown in the smearing of the gradient.

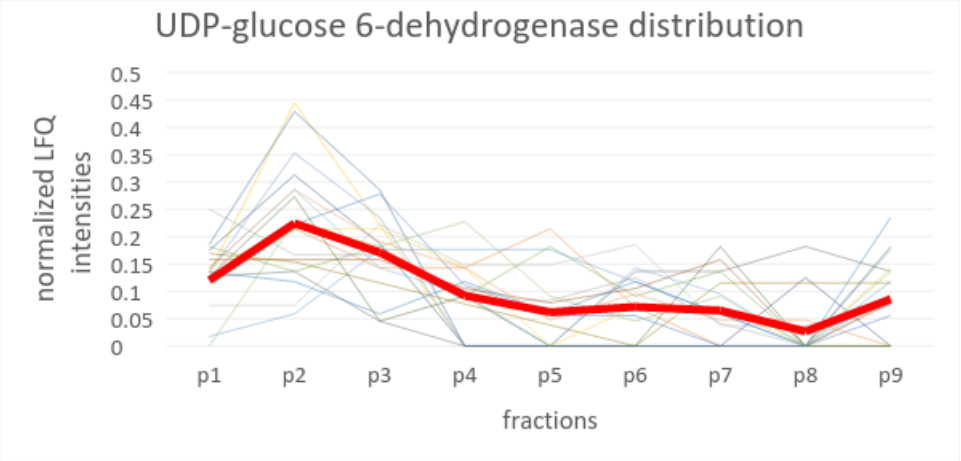


Fig. 13. **UDP-glucose 6-dehydrogenase** behaves in the gradient typically for a cytoplasmatic protein due to its smearing through the whole gradient but with high abundances from p2 to p7. UDP-glucose 6-dehydrogenase is predicted via WoLF PSORT to be located in the cytosol.

4.3.4.3 Vacular fractions

The previously used protein marker, for the vacuolar subcellular compartment Bifunctional purple acid phosphatase 26 was not identified in the whole dataset of the 3. experiment. Instead a new protein marker was identified and used, Nitrate transporter (NTL1). The subcellular prediction of Nitrate transporter (NTL1) was done via WoLF PSORT (Horton et al., 2007) and showed a possible location in the vacuole.

As expected most proteins which were found with a high abundance in the vacuolar fractions were indeed vacuolar associated proteins, but not all, since a lot of fragments were collected at the bottom of the gradient. Therefore, a lot of low abundance noise was found at the last fraction.

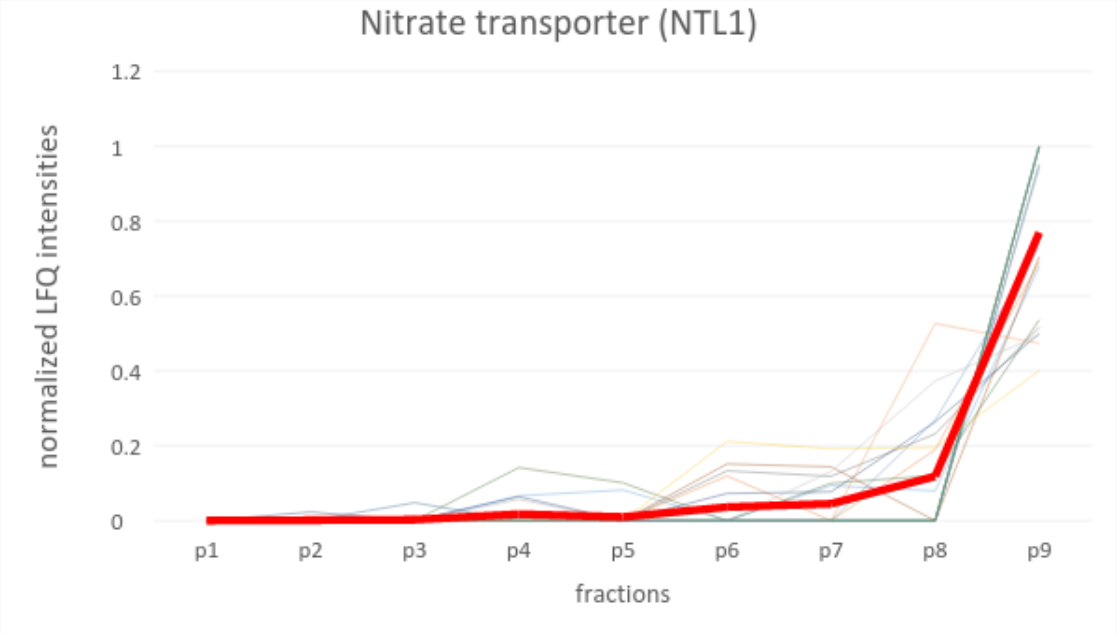


Fig. 14. **Nitrate transporter (NTL1)** was taken due to the unidentifiability of the previous marker protein, the Bifunctional purple acid phosphatase 26. Nitrate transporter (NTL1) is predicted to be a located in the vacuole.

4.3.5 Different proteins found in healthy and infected plants

A Venn-diagram shows the overlap of the uniquely expressed proteins in both healthy and Infected plants. The small overlap of 438proteins shows the expression shift from the pathogen-infection and therefor possibly the defensive reaction. However only proteins were considered which were found in every sample of the 3rd experiment, because lots of proteins weren't found in every sample, therefore this diagram perhaps would have lost accuracy.

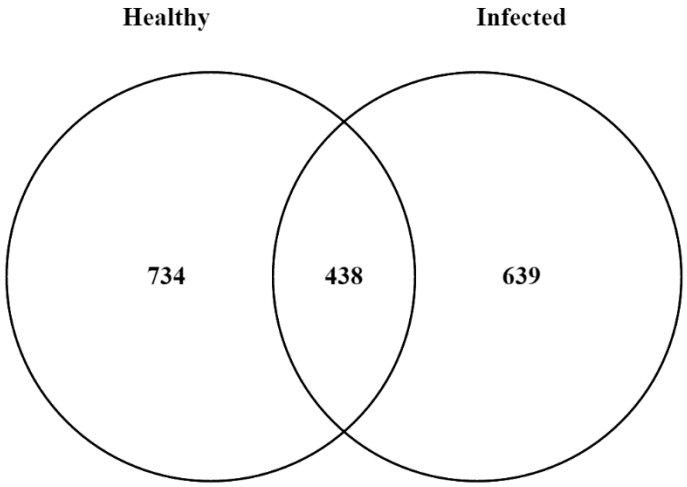
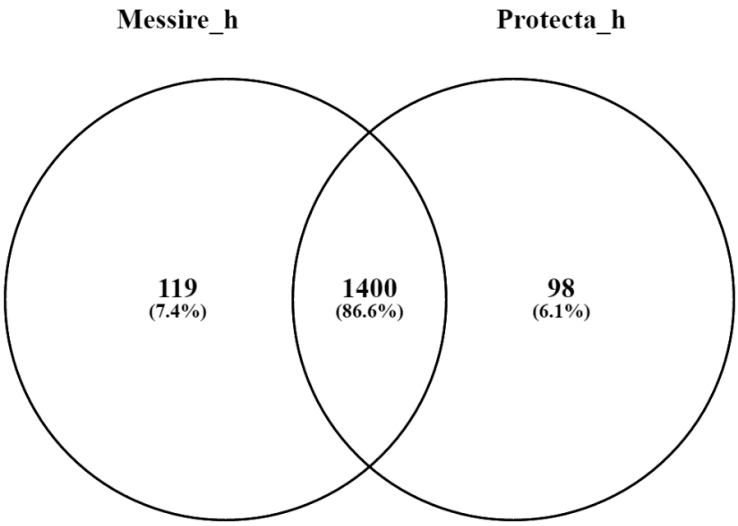


Fig. 15. **Venn-diagram of infected and healthy**

Only proteins which were exclusively found in every sample were considered for this Venn-diagram.

4.3.6 Different proteins found in cultivar Protecta and Messire

The Venn-diagram shows the different proteins found between the cultivars Protecta and Messire. The overlap of 1400 proteins shows that the majority of the proteins which were



found are expressed in both cultivars and only 217 proteins are expressed either in Messire or Protecta. Again only proteins were used which were found in every sample of the 3. experiment.

Fig. 16. Venn-diagram if the Messire and Protecta cultivars showing on overlap of 1400proteins.

4.3.7 Venn-diagram based on the clustering via Matlab

Matlab was used to cluster (as seen in Fig.17) every gradient to identify proteins which were localized in the same subcellular location. Therefore, abundant proteins which were only visible in certain fractions (e.g. 1+2 for chloroplast related proteins) were marked as chloroplast-associated proteins. The same procedure was used for cytosolic and vacuolar proteins.

For this Venn-diagram the whole dataset of every gradient was used(Exp.3) but only unique proteins were counted. Even though the cytoplasm and the vacuole proteins are quite rare, the cutting quantities were also considered.

The 834 shared proteins between the plastid-fractions and the cytoplasm-fractions are the most difficult to determine regarding to their specific location since the cytoplasm-related proteins tend to smear through the whole gradient. This is also seen in Fig.12 when viewing at the marker proteins for the cytoplasm. The marker is found in cytoplasmic regions

of the gradient as well as in vacuolar regions. On the other hand, proteins which are found exclusively in the plastid fractions are presumably located in the chloroplasts.

Only 5 proteins could be determined as vacuole-located, but the shared 69 proteins are probably related as well to the vacuole-proteins. As seen in Fig.13 the marker protein for the vacuole are easier to assign to a specific subcellular location since it's not as blurred as the cytoplasmic marker protein but still it's clearly visible that although the highest abundance is found in the p9 fraction, traces are already found in lower fractions like p5.

The biggest group of proteins are found in every compartment at least once, which makes up for the 1448 proteins. 20 gradients were considered for the clustering and diagram, this high number probably shows the unequal distribution of proteins in the gradient.

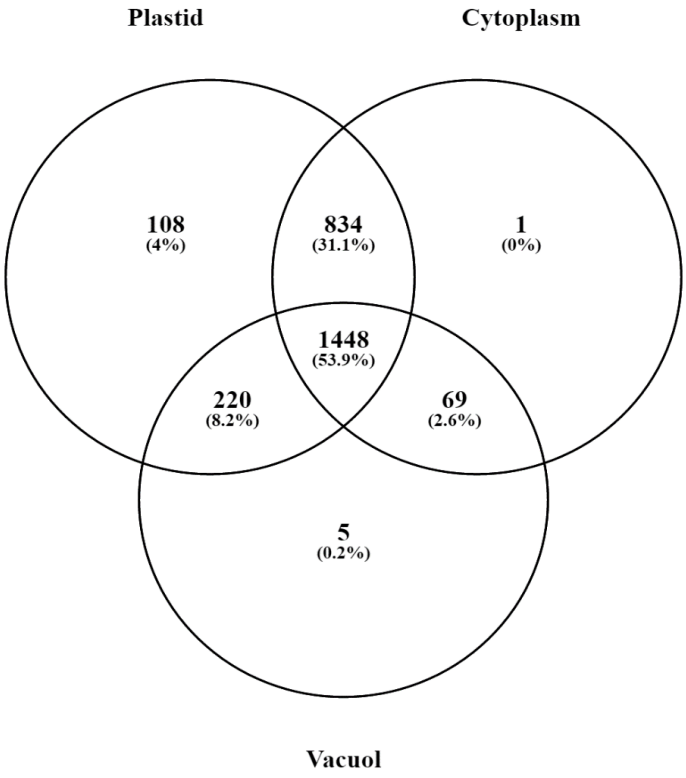


Fig. 17. Venn-diagram of the localization of every protein in Exp.3

4.3.8 Reaction of photosystem-related proteins

A decrease of the intensities of proteins related to the photosystem was detected as well as a shift from clearly a chloroplast-subcellular location to a cytoplasmic location.

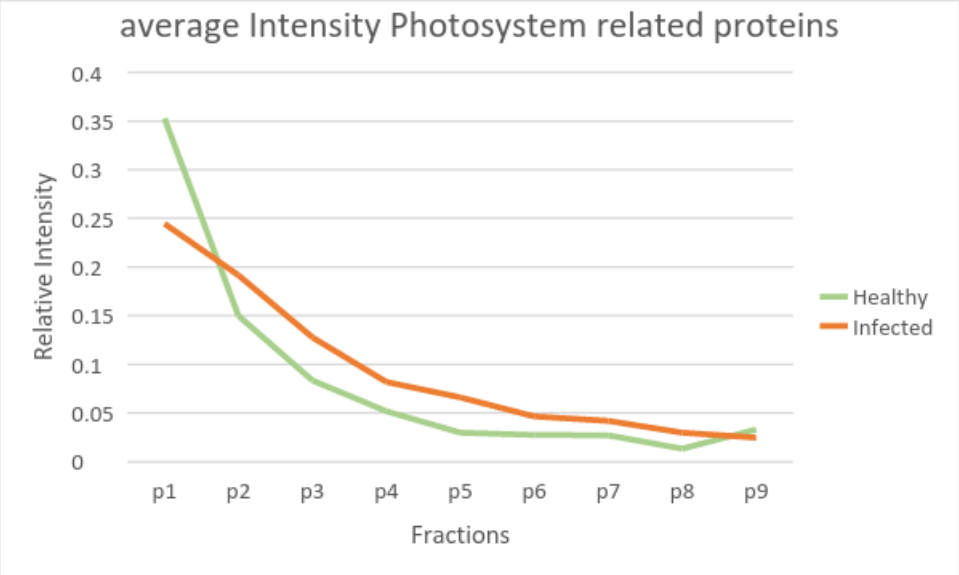


Fig. 18. **Proteins related to the photosystem in healthy and infected plants**

4.3.9 Clustering of the fractions based on the LFQ intensities

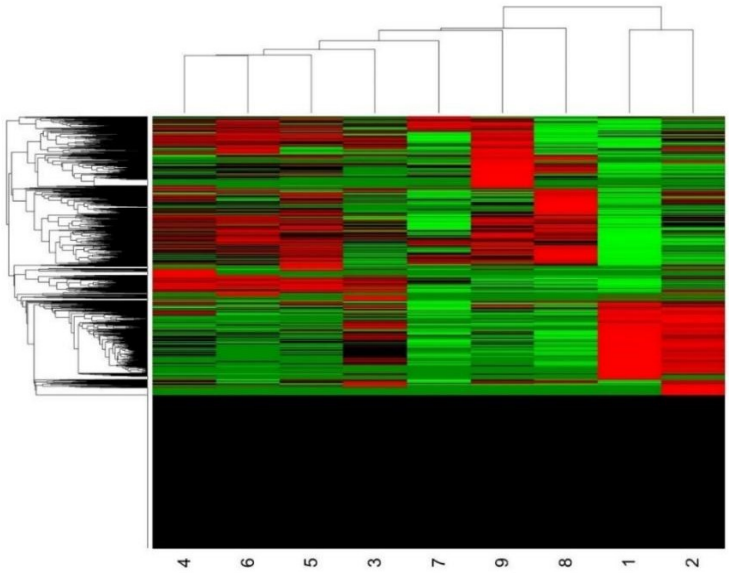


Fig. 19. **Clustergram of the plant sample in gradient 67**

The color code of red and green indicates whether proteins are abundant or not. The more two fractions have in common regarding similarity in identified proteins all the closer they are clustered.

Clearly visible was the relative proximity of the first two fractions, more precisely fraction 1 and 2 at the far-right end. They were clearly distinguishable from all other fractions which indicated a successful separation of the chloroplast associated proteins. The fractions 8 and 9 which respectively represent proteins from the vacuole as well as proteins which were clustering with this compartment were clearly separated from the cytosolic fractions which range from fraction 3 to 7.
This clear separation of the subcellular compartments in gradient 67 indicated a successful non-aqueous fractionation, although it didn't show or gave information, if the proteins were really located or at least predicted in the chloroplasts.

5. Discussion

5.1 Use of non-aqueous fractionation for determining subcellular location for *Pisum sativum* proteins.

The non-aqueous fractionation coupled with MS analysis has the possibility to determine the exact subcellular location of every single protein in a specific proteome as a high-throughput method. Also, it allows to show relative and absolute quantities of a protein to any given point of time, making it possible to determine changes in protein levels due to environmental influences.

First, the technique to correctly annotate protein location can help to improve wrongly assigned protein locations by false predictions. Such as LHCB-1 was predicted to be a mitochondrial associated protein but no hits were found in the associated fractions. Instead the highest abundance was found in p8+p9. In the next step, it would be crucial to determine whether it clusters with vacuolic proteins or is wrongly annotated.

The strength of the non-aqueous fractionation could also be its weakness. Like the clear separation of the proteins from the chloroplasts and all related clustering proteins but on the other side, proteins presumable located in the cytosol are especially found in the middle fractions like p2-p7 and therefore are hard to definitely assign to a specific compartment.

The final fraction, p9 with mostly vacuole proteins is clearly distinguishable from the rest of the clusters. But a closer look at the peptides (and their quantities) allows no clear determination of the subcellular location.

Even clearly annotated proteins which were assigned to a specific subcellular compartment overlapped through multiple fractions and could not be resolved. This is well recognizable in the paper of Arrivault et al. in which proteins are divided into 10 compartments. Clearly visible are 3 major trends, the plastid proteins which have the highest abundance in the first 3 fractions but nevertheless tend to smear through the gradient. The cytosol associated proteins tend to follow absolutely no rules, regarding their tendencies to be in every fraction such as the UDP-glucose 6-dehydrogenase. Only the vacuole proteins tend to have high abundancies in the last fraction again. (Arrivault et al., 2014)

A reason for this smear-effect of the cytosol-related proteins could be the relatively low abundance of absolute amount protein in the fraction p3-p8. The Bradford assay

(Bradford, 1976) showed relatively low absolute protein amount. Most of the absolute quantity of proteins were found in p1 and p2 as well as p9, which is no surprise since this probably proofs, that chloroplast associated proteins such as RuBisCO, which is one of the most abundant proteins on earth, are the most abundant in a plant cell.
One downside in protein analysis and as well as in the non-aqueous fractionation is, if performed with an incomplete proteome database such as *Pisum sativum* the number of detectable peptides is limited, because most annotation of the identified proteins are still unclear. Probably a non-aqueous fractionation would tend to be more meaningful when a proteome which is already fully annotated is used, such as A. thaliana with the TAIR database.(Huala et al., 2001)
For a more clear separation of the cellular organelles and increase of the resolution the increase will most likely not yield the result as shown by Arrivault et al. but the reason for that could lie in the heterogeneity of the cell due to the still not completely understood principle of the clustering of subcellular proteins during the NAF.(Arrivault et al., 2014)

5.2 Overlap infected and healthy

The overlap in Fig.14 shows 639 proteins which are exclusively found in infected plants, that could indicate proteins which are upregulated when a pathogen attacks, is perceived by the plant. In Fig.18 in the attachments a more detailed Venn-diagram takes the 2 different cultivars in account and shows 44 unique proteins for the infection in Messire and 26 unique proteins in the infection in Protecta.

5.3 Use of marker proteins or clustergrams for evaluation of gradients

Marker proteins have a great advantage in contrast to clustergrams as shown in Fig.X regarding the confirmation of the subcellular location of identified proteins. Marker proteins are mostly annotated proteins which are confirmed to be found in a specific compartment and therefore provide information by their distribution in the density gradient. Since proteins in a similar subcellular compartment as the marker proteins should behave in a similar manner like the marker proteins, their fractionation patterns should also be the same. By this pattern of distribution, it should be possible to validate the subcellular location of most proteins identified via a non-aqueous fractionation. The downside of marker proteins is, if the eukaryote which is analyzed doesn't have a complete annotated proteome and therefore the subcellular locations of most proteins are mainly calculated. In addition, the protein identification rate due to smaller databases increases the difficulty of finding stable marker proteins for evaluating if the non-aqueous fractionation was suc-

cessful and therefore the gradient is useable for furtherer analysis.
At this point the clustergram could reveal a first insight if the different fractions are clustering as expected like seen in Fig.19 with gradient 67. The clear clustering of chloroplast as well as vacuole fractions and in the middle the cytosolic fractions.

5.4 Proteins related to photosynthesis respond to a pathogen attack

A higher count of fractions does not necessarily yield a higher resolution in the separation as shown by Arrivaul et.al. (Arrivault et al., 2014) The majority of the subcellular compartments can't be reliable and reproducible be located in the very same fractions over the whole experiment. Variations due to technical difficulties as well as the sensitive nature of the density gradient, starting with pouring the gradient, loading it and as well as taking off the fractions are having a higher impact on those results than the actual distribution of the proteins.

5.5 Proteins related to photosynthesis respond to a pathogen attack

Plants tend to decrease secondary and primary metabolism when infected with a pathogen. While defense programs are upregulated photosynthesis is downregulated and therefore can cause a loss in crop yield. (Berger, Sinha, & Roitsch, 2007) Infected leaves have reduced rates of photosynthesis and therefore the chloroplast-related proteins should be less abundant. (Kocal, Sonnewald, & Sonnewald, 2008) Proteins such as the LHCB-1 are clearly downregulated in the infected plants. This protein could therefore indicate a decrease in photosynthesis. The decrease could be due to loss of leaf-area or redistribution nutrients to benefit the pathogen and ultimately could lead to the suppression of the plants defensive response.(Kocal et al., 2008)
On the other hand proteins related to the defense mechanics against pathogen are clearly upregulated such as callose to strengthen cellwalls.

6. Conclusion and Outlook

The non-aqueous fractionation coupled with the LS-MS is a technique with a wide applicability to identify and specifically locate proteins. Until now the determination of the subcellular location of proteins was only possible with great effort or only predictable via bioinformatic tools. The advantage of NAF lies in its scalability to identify and locate a massive amount of proteins simultaneously. A complete or almost complete proteome allows a quick identification and analyzation and is therefore a prerequisite.

The biggest limitation of NAF is probably the separation of the cytosol and therefore the indistinguishability of proteins associated to mitochondrion, nucleus, peroxisome and the endoplasmic reticulum. To separate those subcellular organelles a higher resolution needs to be achieved.

The absolute quantification with isotope labeled standard proteins would allow the calculation of the exact fluctuation between different treatments as well as between organelles even in a specific timeframe. The redistribution of proteins could be watched in specific points of time after the infection.

Furthermore, NAF allows for the calculation of the fluctuation of proteins and metabolite levels between different subcellular organelles. To absolutely quantify proteins, isotope labeled standard peptides would need to be used. Marker proteins, which are already confirmed at specific subcellular locations as well as identified in those locations come to mind for such a task.

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8. Attachments

Deutscher Abstrakt

Die „non-aqueous fractionation“ (NAF) wurde entwickelt um Metaboliten zu fraktionieren, basierend auf deren subzellulärer Lage. NAF hatte bereits gezeigt, dass Metaboliten und Proteine gleichzeitig analysiert werden konnten. Die Trennung erlaubt eine höhere Auflösung, wenn via Massenspektrometrie(MS) detektiert wird. Dadurch können subzelluläre Organellen wie Chloroplasten, Cytoplasma und Vakuole sowie ihre begleitenden Metaboliten und

Proteine lokalisiert werden innerhalb der Zelle. Bei Pflanzen, welchem durch ein Pathogen wie *Didymella pinodes* befallen sind, aktivieren ihr Immunsystem in verschiedenen Organellen um gegen den Erreger zu kämpfen. In meiner Masterarbeit untersuchte ich die Reaktion auf das Pathogen auf subzellulärer Proteinebene. Weiters untersuchte ich potentielle Markerproteine für die verschiedenen Zellorganellen. Bei einem pathogenen Befall über *Didymella pinodes* Pflanzen, wie *Pisum sativum*, aktivieren ihr Immunsystem in verschiedenen Organellenstufen gegen den Erreger.

In meiner Masterarbeit untersuchte ich die Reaktion auf das pathogene subzelluläre Proteinniveau. Darüber hinaus untersuchte ich Organelle Markerproteine durch mehrere Experimente.

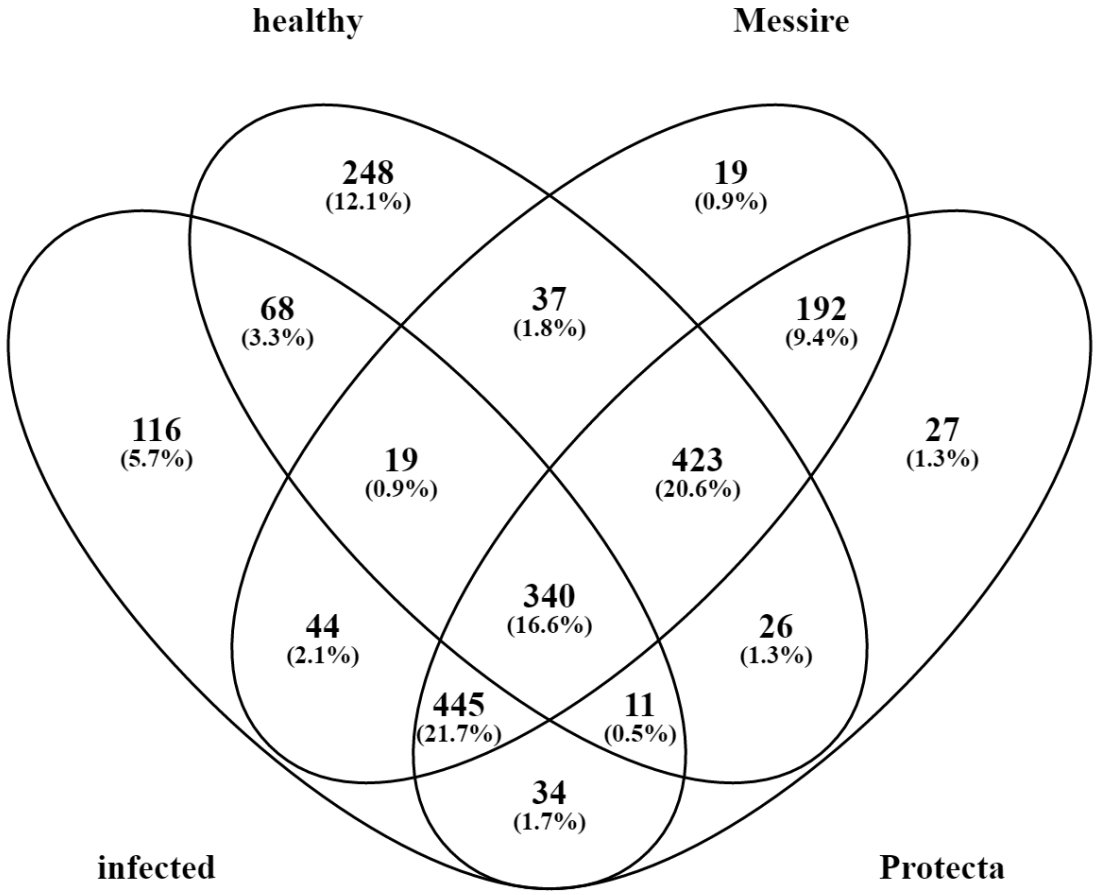

Fig. 20. Venn-diagram showing proteins specific for infected/healthy and Messire/Protecta cultivars.

Venn-Diagram proteins infected/healthy

Unique_inf	Unique_healthy	Both(overlap)
639	734	438

>generic|frv2_21867|franssen_12890_
>gi|3426335|upncbi901 pectin methyl
>generic|frv2_78451|Pisum_sativum_v
>generic|frv2_88369|Pisum_sativum_v
>generic|frv2_45359|franssen_27867_
>generic|frv2_118833|p.sativum_wa1_
>generic|frv2_82689|Pisum_sativum_v
>generic|frv2_10950|franssen_6399_3
>generic|frv2_48720|franssen_29928_
>generic|frv2_114164|p.sativum_wa1_
>generic|frv2_71239|franssen_44043_
>generic|frv2_125039|p.sativum_wa1_
>generic|frv2_55204|franssen_34314_
>generic|frv2_114031|p.sativum_wa1_
>generic|frv2_50609|franssen_31232_
>gi|118150|upncbi2001 RecName: Full
>generic|frv2_74187|Pisum_sativum_v
>generic|frv2_86018|Pisum_sativum_v
>generic|frv2_52729|franssen_32690_
>generic|frv2_15622|franssen_9181_4
>generic|frv2_100730|p.sativum_wa1_
>generic|frv2_78041|Pisum_sativum_v
>generic|frv2_83260|Pisum_sativum_v
>generic|frv2_99187|p.sativum_wa1_c
>generic|frv2_98356|p.sativum_wa1_c
>generic|frv2_80178|Pisum_sativum_v
>generic|frv2_58274|franssen_36157_
>generic|frv2_117042|p.sativum_wa1_
>generic|frv2_113263|p.sativum_wa1_
>generic|frv2_113205|p.sativum_wa1_
>generic|frv2_49931|franssen_30753_
>generic|frv2_59767|franssen_37114_
>generic|frv2_80806|Pisum_sativum_v
>generic|frv2_8512|franssen_4962_1
>generic|frv2_68907|franssen_42484_
>generic|frv2_75016|Pisum_sativum_v
>generic|frv2_83388|Pisum_sativum_v
>generic|frv2_47502|franssen_29127_
>gi|113570|upncbi1932 RecName: Full
>generic|frv2_100427|p.sativum_wa1_
>generic|frv2_100629|p.sativum_wa1_
>generic|frv2_101038|p.sativum_wa1_
>generic|frv2_101292|p.sativum_wa1_
>generic|frv2_101403|p.sativum_wa1_
>generic|frv2_101412|p.sativum_wa1_
>generic|frv2_101519|p.sativum_wa1_
>generic|frv2_101619|p.sativum_wa1_
>generic|frv2_122262|p.sativum_wa1_
>generic|frv2_15631|franssen_9186_4
>generic|frv2_82766|Pisum_sativum_v
>generic|frv2_81102|Pisum_sativum_v
>generic|frv2_82925|Pisum_sativum_v
>generic|frv2_78273|Pisum_sativum_v
>generic|frv2_52831|franssen_32760_
>generic|frv2_113168|p.sativum_wa1_
>generic|frv2_50925|franssen_31453_
>generic|frv2_88606|Pisum_sativum_v
>generic|frv2_67395|franssen_41580_
>generic|frv2_112178|p.sativum_wa1_
>generic|frv2_85601|Pisum_sativum_v
>generic|frv2_124697|p.sativum_wa1_
>generic|frv2_125550|p.sativum_wa1_
>generic|frv2_115202|p.sativum_wa1_
>generic|frv2_79808|Pisum_sativum_v
>generic|frv2_98354|p.sativum_wa1_c
>generic|frv2_101306|p.sativum_wa1_
>generic|frv2_50146|franssen_30905_
>generic|frv2_101773|p.sativum_wa1_
>generic|frv2_102274|p.sativum_wa1_
>generic|frv2_102339|p.sativum_wa1_
>generic|frv2_102711|p.sativum_wa1_
>generic|frv2_103190|p.sativum_wa1_
>generic|frv2_103298|p.sativum_wa1_
>generic|frv2_103365|p.sativum_wa1_
>generic|frv2_103496|p.sativum_wa1_
>generic|frv2_103716|p.sativum_wa1_
>generic|frv2_105010|p.sativum_wa1_
>generic|frv2_107924|p.sativum_wa1_
>generic|frv2_110547|p.sativum_wa1_
>generic|frv2_110742|p.sativum_wa1_
>generic|frv2_111051|p.sativum_wa1_
>generic|frv2_111059|p.sativum_wa1_
>generic|frv2_111105|p.sativum_wa1_
>generic|frv2_111119|p.sativum_wa1_
>generic|frv2_111135|p.sativum_wa1_
>generic|frv2_111298|p.sativum_wa1_
>generic|frv2_111330|p.sativum_wa1_
>generic|frv2_111520|p.sativum_wa1_
>generic|frv2_111576|p.sativum_wa1_
>generic|frv2_111629|p.sativum_wa1_
>generic|frv2_111645|p.sativum_wa1_
>generic|frv2_111652|p.sativum_wa1_
>generic|frv2_111740|p.sativum_wa1_
>generic|frv2_111748|p.sativum_wa1_
>gi|76873802|upncbi1668 putative ba
>generic|frv2_103161|p.sativum_wa1_
>generic|frv2_82380|Pisum_sativum_v
>generic|frv2_112930|p.sativum_wa1_
>generic|frv2_77065|Pisum_sativum_v
>generic|frv2_117707|p.sativum_wa1_
>generic|frv2_40409|franssen_24603_
>generic|frv2_53036|franssen_32908_
>generic|frv2_112169|p.sativum_wa1_
>gi|13359453|upncbi1418 putative se
>generic|frv2_101401|p.sativum_wa1_
>generic|frv2_115020|p.sativum_wa1_
>gi|114260|upncbi1979 RecName: Full
>generic|frv2_110573|p.sativum_wa1_
>generic|frv2_101837|p.sativum_wa1_
>generic|frv2_103634|p.sativum_wa1_
>generic|frv2_104859|p.sativum_wa1_
>generic|frv2_105035|p.sativum_wa1_
>generic|frv2_107818|p.sativum_wa1_
>generic|frv2_110916|p.sativum_wa1_
>generic|frv2_111145|p.sativum_wa1_
>generic|frv2_111189|p.sativum_wa1_
>generic|frv2_111200|p.sativum_wa1_
>generic|frv2_111415|p.sativum_wa1_
>generic|frv2_111525|p.sativum_wa1_
>generic|frv2_111604|p.sativum_wa1_
>generic|frv2_111622|p.sativum_wa1_
>generic|frv2_111637|p.sativum_wa1_
>generic|frv2_111647|p.sativum_wa1_
>generic|frv2_111795|p.sativum_wa1_
>generic|frv2_111833|p.sativum_wa1_
>generic|frv2_111928|p.sativum_wa1_
>generic|frv2_112360|p.sativum_wa1_
>generic|frv2_112438|p.sativum_wa1_
>generic|frv2_112512|p.sativum_wa1_
>generic|frv2_112647|p.sativum_wa1_
>generic|frv2_112683|p.sativum_wa1_
>generic|frv2_112849|p.sativum_wa1_
>generic|frv2_11288|franssen_6609_3
>generic|frv2_113499|p.sativum_wa1_
>generic|frv2_113814|p.sativum_wa1_
>generic|frv2_113825|p.sativum_wa1_
>generic|frv2_113828|p.sativum_wa1_
>generic|frv2_113940|p.sativum_wa1_
>generic|frv2_114208|p.sativum_wa1_
>generic|frv2_114924|p.sativum_wa1_
>generic|frv2_115027|p.sativum_wa1_

>generic|frv2_101817|p.sativum_wa1_
>generic|frv2_101984|p.sativum_wa1_
>generic|frv2_102267|p.sativum_wa1_
>generic|frv2_102358|p.sativum_wa1_
>generic|frv2_102386|p.sativum_wa1_
>generic|frv2_102436|p.sativum_wa1_
>generic|frv2_102659|p.sativum_wa1_
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>generic|frv2_103257|p.sativum_wa1_
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>generic|frv2_109914|p.sativum_wa1_
>generic|frv2_110751|p.sativum_wa1_
>generic|frv2_110841|p.sativum_wa1_
>generic|frv2_110858|p.sativum_wa1_
>generic|frv2_110926|p.sativum_wa1_
>generic|frv2_110980|p.sativum_wa1_
>generic|frv2_111007|p.sativum_wa1_
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>generic|frv2_113132|p.sativum_wa1_
>generic|frv2_113162|p.sativum_wa1_
>generic|frv2_113199|p.sativum_wa1_
>generic|frv2_113630|p.sativum_wa1_
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>generic|frv2_48143|franssen_29532_
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>generic|frv2_48468|franssen_29755_
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>generic|frv2_48598|franssen_29847_
>generic|frv2_48636|franssen_29871_
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>generic|frv2_49270|franssen_30297_

>generic|frv2_111933|p.sativum_wa1_
>generic|frv2_112029|p.sativum_wa1_
>generic|frv2_112035|p.sativum_wa1_
>generic|frv2_112095|p.sativum_wa1_
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>generic|frv2_112796|p.sativum_wa1_
>generic|frv2_112903|p.sativum_wa1_
>generic|frv2_1130|franssen_658_1 P
>generic|frv2_113057|p.sativum_wa1_
>generic|frv2_113344|p.sativum_wa1_
>generic|frv2_113406|p.sativum_wa1_
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>generic|frv2_117630|p.sativum_wa1_
>generic|frv2_117668|p.sativum_wa1_
>generic|frv2_117990|p.sativum_wa1_
>generic|frv2_11802|franssen_6912_5
>generic|frv2_118137|p.sativum_wa1_
>generic|frv2_118953|p.sativum_wa1_
>generic|frv2_119383|p.sativum_wa1_
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>generic|frv2_121037|p.sativum_wa1_
>generic|frv2_121521|p.sativum_wa1_
>generic|frv2_12154|franssen_7125_2
>generic|frv2_128142|p.sativum_wa1_
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>generic|frv2_135271|p.sativum_wa1_
>generic|frv2_23868|franssen_14120_
>generic|frv2_27909|franssen_16426_
>generic|frv2_31391|franssen_18456_
>generic|frv2_44509|franssen_27393_
>generic|frv2_4471|franssen_2602_5
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>generic|frv2_45969|franssen_28214_
>generic|frv2_46003|franssen_28233_
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>generic|frv2_46140|franssen_28314_
>generic|frv2_46274|franssen_28389_
>generic|frv2_46407|franssen_28469_
>generic|frv2_46644|franssen_28610_
>generic|frv2_46758|franssen_28674_
>generic|frv2_46778|franssen_28684_
>generic|frv2_47292|franssen_28990_
>generic|frv2_47306|franssen_28999_
>generic|frv2_47309|franssen_29001_
>generic|frv2_47354|franssen_29030_
>generic|frv2_47383|franssen_29049_
>generic|frv2_47402|franssen_29061_
>generic|frv2_47468|franssen_29106_
>generic|frv2_47545|franssen_29154_
>generic|frv2_47643|franssen_29219_
>generic|frv2_47726|franssen_29271_
>generic|frv2_47921|franssen_29400_
>generic|frv2_47967|franssen_29426_
>generic|frv2_47981|franssen_29434_
>generic|frv2_48293|franssen_29638_
>generic|frv2_48299|franssen_29642_
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ric|mut36|Pisum_sativum_v2_Con
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>gi|119905|upncbi1941 RecName: Full
>gi|121333|upncbi1928 RecName: Full
>gi|12195|upncbi1540 putative zinc-
>gi|1346672|upncbi2048 RecName: Ful
>gi|1351963|upncbi2051 RecName: Ful
>gi|1480347|upncbi1573 ferrodoxin N
>gi|14916975|upncbi2025 RecName:
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>gi|149242527|upncbi797 Chain A, Th
>gi|1703042|upncbi2129 RecName: Ful
>gi|1710807|upncbi1934 RecName: Ful
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>gi|227247874|upncbi1719 unnamed pr
>gi|229365688|upncbi1490 UDP-glucos
>gi|2506277|upncbi1935 RecName: Ful
>gi|257707056|upncbi1736 unnamed pr
>gi|257726091|upncbi1751 unnamed pr
>gi|2605887|upncbi886 dormancy-asso

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>gi|295136984|upncbi2245 ribosomal
>gi|295136993|upncbi2255 photosyste
>gi|300639604|upncbi1815 unnamed pr
>gi|3121727|upncbi2082 RecName: Ful
>gi|34452233|upncbi1053 ripening-re
>gi|3766299|upncbi1525 sucrose synt
>gi|384955577|upncbi2177 RecName: F
>gi|3913218|upncbi1887 RecName: Ful
>gi|3913711|upncbi2083 RecName: Ful
>gi|462187|upncbi2029 RecName: Full
>gi|535444|upncbi851 calmodulin [Pi
>gi|56554368|upncbi789 Chain F, Str
>gi|56809383|upncbi1093 light-harve
>gi|62900628|upncbi2213 RecName: Fu
>gi|62909963|upncbi1474 peroxidase
>gi|729842|upncbi2122 RecName: Full
>gi|7381225|upncbi951 root border c
>gi|73921507|upncbi1911 RecName: Fu
>gi|75150408|upncbi2181 RecName: Fu
>gi|75206752|upncbi2202 RecName: Fu
>gi|75220641|upncbi2130 RecName: Fu
>gi|753534348|upncbi817 Chain F, Cr
>gi|753534353|upncbi820 Chain K, Cr
>gi|753534355|upncbi822 Chain N, Cr
>gi|9968665|upncbi1635 putative ATP
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>gi|1778378|upncbi885 NAP1Ps [Pisum
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>gi|357595281|upncbi1282 chloroplas

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>gi|1708427|upncbi2066 RecName: Ful
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>gi|226088581|upncbi1507 catalase 1
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>gi|290784426|upncbi1800 vicilin 47
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>gi|295136986|upncbi2248 photosyste
>gi|295137000|upncbi2262 NADH dehyd
>gi|295137002|upncbi2264 NADH dehyd
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>gi|310753569|upncbi1261 mutant gag
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>gi|38232568|upncbi1068 translation
>gi|50400709|upncbi1908 RecName: Fu
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>gi|550544719|upncbi810 Chain V, St
>gi|550553961|upncbi1874 unnamed pr
>gi|399082|upncbi2120 RecName: Full
>gi|61611729|upncbi1116 FVE [Pisum
>gi|6624721|upncbi1622 putative cys
>gi|6651031|upncbi946 gamma-
glutamy
>gi|730557|upncbi2037 RecName: Full
>gi|75216541|upncbi2216 RecName:
Fu
>gi|75221490|upncbi2167 RecName:
Fu
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>gi|753534356|upncbi811 Chain 1, Cr
>generic|frv2_101273|p.sativum_wa1_
>generic|frv2_102979|p.sativum_wa1_
>generic|frv2_110760|p.sativum_wa1_
>generic|frv2_111485|p.sativum_wa1_
>generic|frv2_113882|p.sativum_wa1_
>generic|frv2_114337|p.sativum_wa1_
>generic|frv2_122113|p.sativum_wa1_
>generic|frv2_124175|p.sativum_wa1_
>generic|frv2_18104|franssen_10671_
>generic|frv2_31658|franssen_18602_
>generic|frv2_41815|franssen_25529_
>generic|frv2_46376|franssen_28448_
>generic|frv2_46857|franssen_28730_
>generic|frv2_47003|franssen_28813_
>generic|frv2_47431|franssen_29081_
>generic|frv2_47842|franssen_29347_
>generic|frv2_49079|franssen_30170_
>generic|frv2_49168|franssen_30234_
>generic|frv2_49745|franssen_30622_
>generic|frv2_50390|franssen_31079_
>generic|frv2_50780|franssen_31353_
>generic|frv2_51333|franssen_31740_
>generic|frv2_51485|franssen_31835_
>generic|frv2_51935|franssen_32144_
>generic|frv2_53055|franssen_32920_
>generic|frv2_5316|franssen_3094_5
>generic|frv2_54274|franssen_33721_
>generic|frv2_57383|franssen_35646_
>generic|frv2_6068|franssen_3522_6
>generic|frv2_64403|franssen_39843_
>generic|frv2_64954|franssen_40160_
>generic|frv2_68928|franssen_42499_
>generic|frv2_69041|franssen_42568_
>generic|frv2_74723|Pisum_sativum_v
>generic|frv2_74837|Pisum_sativum_v

>generic|frv2_75353|Pisum_sativum_v
>generic|frv2_75390|Pisum_sativum_v
>generic|frv2_75507|Pisum_sativum_v
>generic|frv2_75630|Pisum_sativum_v
>generic|frv2_75936|Pisum_sativum_v
>generic|frv2_76076|Pisum_sativum_v
>generic|frv2_7608|franssen_4439_5
>generic|frv2_76158|Pisum_sativum_v
>generic|frv2_76407|Pisum_sativum_v
>generic|frv2_76491|Pisum_sativum_v
>generic|frv2_76498|Pisum_sativum_v
>generic|frv2_76650|Pisum_sativum_v
>generic|frv2_76675|Pisum_sativum_v
>generic|frv2_76756|Pisum_sativum_v
>generic|frv2_76790|Pisum_sativum_v
>generic|frv2_76811|Pisum_sativum_v
>generic|frv2_76892|Pisum_sativum_v
>generic|frv2_76999|Pisum_sativum_v
>generic|frv2_77026|Pisum_sativum_v
>generic|frv2_77076|Pisum_sativum_v
>generic|frv2_77114|Pisum_sativum_v
>generic|frv2_77257|Pisum_sativum_v
>generic|frv2_77277|Pisum_sativum_v
>generic|frv2_77477|Pisum_sativum_v
>generic|frv2_77558|Pisum_sativum_v
>generic|frv2_77570|Pisum_sativum_v
>generic|frv2_77651|Pisum_sativum_v
>generic|frv2_77785|Pisum_sativum_v
>generic|frv2_77957|Pisum_sativum_v
>generic|frv2_78078|Pisum_sativum_v
>generic|frv2_78131|Pisum_sativum_v
>generic|frv2_78155|Pisum_sativum_v
>generic|frv2_78474|Pisum_sativum_v
>generic|frv2_78667|Pisum_sativum_v
>generic|frv2_78687|Pisum_sativum_v
>generic|frv2_78754|Pisum_sativum_v
>generic|frv2_78786|Pisum_sativum_v
>generic|frv2_78865|Pisum_sativum_v
>generic|frv2_79070|Pisum_sativum_v
>generic|frv2_79466|Pisum_sativum_v
>generic|frv2_79785|Pisum_sativum_v
>generic|frv2_79964|Pisum_sativum_v
>generic|frv2_80049|Pisum_sativum_v
>generic|frv2_80154|Pisum_sativum_v
>generic|frv2_80212|Pisum_sativum_v
>generic|frv2_80226|Pisum_sativum_v
>gi|552817|upncbi847 cytochrome f (
>gi|58038194|upncbi1681 alpha-dioxy
>gi|585454|upncbi2127 RecName: Full
>gi|62909961|upncbi1473 peroxidase
>gi|75098146|upncbi1895 RecName: Fu
>gi|75221107|upncbi2145 RecName: Fu
>gi|84626066|upncbi1146 putative co
>sp|CAS2BOVIN|con4 contaminant4
>sp|K1C10HUMAN|con9 contaminant9
>sp|K1C9HUMAN|con11 contaminant11
>sp|K2C1HUMAN|con24 contaminant24
>sp|LYSCLYSEN|con45 contaminant45
>generic|frv2_109379|p.sativum_wa1_
>generic|frv2_110946|p.sativum_wa1_
>generic|frv2_111004|p.sativum_wa1_
>generic|frv2_111040|p.sativum_wa1_
>generic|frv2_111079|p.sativum_wa1_
>generic|frv2_111349|p.sativum_wa1_
>generic|frv2_111373|p.sativum_wa1_
>generic|frv2_111453|p.sativum_wa1_
>generic|frv2_111675|p.sativum_wa1_
>generic|frv2_111696|p.sativum_wa1_
>generic|frv2_114062|p.sativum_wa1_
>generic|frv2_114753|p.sativum_wa1_
>generic|frv2_114807|p.sativum_wa1_
>generic|frv2_115141|p.sativum_wa1_
>generic|frv2_115271|p.sativum_wa1_
>generic|frv2_116067|p.sativum_wa1_
>generic|frv2_116158|p.sativum_wa1_
>generic|frv2_116576|p.sativum_wa1_
>generic|frv2_117858|p.sativum_wa1_
>generic|frv2_120827|p.sativum_wa1_
>generic|frv2_121399|p.sativum_wa1_
>generic|frv2_123118|p.sativum_wa1_
>generic|frv2_124975|p.sativum_wa1_
>generic|frv2_125650|p.sativum_wa1_
>generic|frv2_126055|p.sativum_wa1_
>generic|frv2_128280|p.sativum_wa1_
>generic|frv2_128411|p.sativum_wa1_
>generic|frv2_13778|franssen_8089_6
>generic|frv2_15380|franssen_9043_1
>generic|frv2_22975|franssen_13586_
>generic|frv2_2539|franssen_1495_6
>generic|frv2_26330|franssen_15510_
>generic|frv2_41448|franssen_25293_
>generic|frv2_46225|franssen_28360_
>generic|frv2_74959|Pisum_sativum_v
>generic|frv2_76015|Pisum_sativum_v
>generic|frv2_76542|Pisum_sativum_v
>generic|frv2_76807|Pisum_sativum_v
>generic|frv2_76819|Pisum_sativum_v
>generic|frv2_77969|Pisum_sativum_v
>generic|frv2_78698|Pisum_sativum_v
>generic|frv2_79797|Pisum_sativum_v
>generic|frv2_80547|Pisum_sativum_v
>generic|frv2_82045|Pisum_sativum_v
>generic|frv2_82054|Pisum_sativum_v
>generic|frv2_82718|Pisum_sativum_v
>generic|frv2_83390|Pisum_sativum_v
>generic|frv2_84193|Pisum_sativum_v
>generic|frv2_84514|Pisum_sativum_v
>generic|frv2_84566|Pisum_sativum_v
>generic|frv2_86596|Pisum_sativum_v
>generic|frv2_88944|Pisum_sativum_v
>generic|frv2_90447|Pisum_sativum_v
>generic|frv2_91750|FG534173_1 shor
>generic|frv2_93642|GH720733_6 MULT
>generic|frv2_95733|p.sativum_wa1_c
>generic|frv2_97144|p.sativum_wa1_c
>generic|frv2_99479|p.sativum_wa1_c
>generic|mut47|p.sativum_wa1_contig
>gi|118514|upncbi2000 RecName: Full
>gi|131390|upncbi1965 RecName: Full
>gi|442571760|upncbi1332 histone H1

>generic|frv2_80239|Pisum_sativum_v
>generic|frv2_80254|Pisum_sativum_v
>generic|frv2_80261|Pisum_sativum_v
>generic|frv2_80273|Pisum_sativum_v
>generic|frv2_80362|Pisum_sativum_v
>generic|frv2_80365|Pisum_sativum_v
>generic|frv2_80392|Pisum_sativum_v
>generic|frv2_80442|Pisum_sativum_v
>generic|frv2_80525|Pisum_sativum_v
>generic|frv2_80600|Pisum_sativum_v
>generic|frv2_80689|Pisum_sativum_v
>generic|frv2_80801|Pisum_sativum_v
>generic|frv2_80866|Pisum_sativum_v
>generic|frv2_80879|Pisum_sativum_v
>generic|frv2_80944|Pisum_sativum_v
>generic|frv2_80964|Pisum_sativum_v
>generic|frv2_81021|Pisum_sativum_v
>generic|frv2_81121|Pisum_sativum_v
>generic|frv2_81144|Pisum_sativum_v
>generic|frv2_81212|Pisum_sativum_v
>generic|frv2_81292|Pisum_sativum_v
>generic|frv2_81301|Pisum_sativum_v
>generic|frv2_81331|Pisum_sativum_v
>generic|frv2_81378|Pisum_sativum_v
>generic|frv2_81411|Pisum_sativum_v
>generic|frv2_81466|Pisum_sativum_v
>generic|frv2_81576|Pisum_sativum_v
>generic|frv2_81614|Pisum_sativum_v
>generic|frv2_81655|Pisum_sativum_v
>generic|frv2_81662|Pisum_sativum_v
>generic|frv2_81743|Pisum_sativum_v
>generic|frv2_81771|Pisum_sativum_v
>generic|frv2_81821|Pisum_sativum_v
>generic|frv2_81982|Pisum_sativum_v
>generic|frv2_82020|Pisum_sativum_v
>generic|frv2_82257|Pisum_sativum_v
>generic|frv2_82267|Pisum_sativum_v
>generic|frv2_82389|Pisum_sativum_v
>generic|frv2_82402|Pisum_sativum_v
>generic|frv2_82459|Pisum_sativum_v
>generic|frv2_82483|Pisum_sativum_v
>generic|frv2_82521|Pisum_sativum_v
>generic|frv2_82528|Pisum_sativum_v
>generic|frv2_82621|Pisum_sativum_v
>generic|frv2_82624|Pisum_sativum_v
>generic|frv2_82891|Pisum_sativum_v
>generic|frv2_82904|Pisum_sativum_v
>generic|frv2_47256|franssen_28968_
>generic|frv2_47759|franssen_29292_
>generic|frv2_49049|franssen_30149_
>generic|frv2_49395|franssen_30382_
>generic|frv2_49499|franssen_30453_
>generic|frv2_49898|franssen_30729_
>generic|frv2_50403|franssen_31088_
>generic|frv2_50482|franssen_31147_
>generic|frv2_50632|franssen_31250_
>generic|frv2_51580|franssen_31896_
>generic|frv2_52145|franssen_32295_
>generic|frv2_52681|franssen_32656_
>generic|frv2_55043|franssen_34211_
>generic|frv2_56831|franssen_35329_
>generic|frv2_58302|franssen_36172_
>generic|frv2_58737|franssen_36432_
>generic|frv2_60220|franssen_37413_
>generic|frv2_63032|franssen_39065_
>generic|frv2_66384|franssen_40993_
>generic|frv2_68431|franssen_42190_
>generic|frv2_68954|franssen_42516_
>generic|frv2_74598|Pisum_sativum_v
>generic|frv2_76113|Pisum_sativum_v
>generic|frv2_77264|Pisum_sativum_v
>generic|frv2_77294|Pisum_sativum_v
>generic|frv2_79240|Pisum_sativum_v
>generic|frv2_79740|Pisum_sativum_v
>generic|frv2_80164|Pisum_sativum_v
>generic|frv2_80803|Pisum_sativum_v
>generic|frv2_80970|Pisum_sativum_v
>generic|frv2_81214|Pisum_sativum_v
>generic|frv2_81282|Pisum_sativum_v
>generic|frv2_81491|Pisum_sativum_v
>generic|frv2_81620|Pisum_sativum_v
>generic|frv2_81755|Pisum_sativum_v
>generic|frv2_82038|Pisum_sativum_v
>generic|frv2_83421|Pisum_sativum_v
>generic|frv2_83496|Pisum_sativum_v
>generic|frv2_83745|Pisum_sativum_v
>generic|frv2_86555|Pisum_sativum_v
>generic|frv2_87460|Pisum_sativum_v
>generic|frv2_87472|Pisum_sativum_v
>generic|frv2_90748|Pisum_sativum_v
>generic|frv2_95392|p.sativum_wa1_c
>generic|frv2_95822|p.sativum_wa1_c
>gi|122937805|upncbi1166 yieldin-li
>gi|267120|upncbi2015 RecName: Full

>generic|frv2_82930|Pisum_sativum_v	>gi|37051111|upncbi1451 short-chain
>generic|frv2_83056|Pisum_sativum_v	>gi|18375|upncbi1590 dehydrin-cogna
>generic|frv2_83143|Pisum_sativum_v	>gi|24417715|upncbi1019 antimicrobi
>generic|frv2_83257|Pisum_sativum_v	>gi|257632903|upncbi1772 unnamed pr
>generic|frv2_83291|Pisum_sativum_v	>gi|257673606|upncbi1755 unnamed pr
>generic|frv2_83358|Pisum_sativum_v	>gi|257676001|upncbi1782 unnamed pr
>generic|frv2_83447|Pisum_sativum_v	>gi|267075|upncbi2017 RecName: Full
>generic|frv2_83733|Pisum_sativum_v	>gi|295136983|upncbi2244 NADH dehyd
>generic|frv2_83850|Pisum_sativum_v	>gi|295136999|upncbi2261 ribosomal
>generic|frv2_84010|Pisum_sativum_v	>gi|295137005|upncbi2267 photosyste
>generic|frv2_84113|Pisum_sativum_v	>gi|295137036|upncbi2297 RNA polyme
>generic|frv2_84123|Pisum_sativum_v	>gi|295137037|upncbi2298 ribosomal
>generic|frv2_84179|Pisum_sativum_v	>gi|295137048|upncbi2246 photosyste
>generic|frv2_84513|Pisum_sativum_v	>gi|298552527|upncbi1811 unnamed pr
>generic|frv2_84684|Pisum_sativum_v	>gi|3116020|upncbi1586 FtsZ protein
>generic|frv2_85002|Pisum_sativum_v	>gi|357595287|upncbi1285 chloroplas
>generic|frv2_85005|Pisum_sativum_v	>gi|363806029|upncbi1846 Histone H1
>generic|frv2_85077|Pisum_sativum_v	>gi|37051117|upncbi1454 S-adenosylm
>generic|frv2_85135|Pisum_sativum_v	>gi|3893097|upncbi1534 unnamed prot
>generic|frv2_85437|Pisum_sativum_v	>gi|41222521|upncbi1670 phytoene de
>generic|frv2_85514|Pisum_sativum_v	>gi|461753|upncbi2031 RecName: Full
>generic|frv2_85867|Pisum_sativum_v	>gi|498906|upncbi850 ribosomal prot
>generic|frv2_85885|Pisum_sativum_v	>gi|6016132|upncbi2151 RecName: Ful
>generic|frv2_86036|Pisum_sativum_v	>gi|6092014|upncbi1398 hsr203J homo
>generic|frv2_86115|Pisum_sativum_v	>gi|625990|upncbi1380 porin, plasti
>generic|frv2_86230|Pisum_sativum_v	>gi|62909957|upncbi1471 peroxidase
>generic|frv2_86258|Pisum_sativum_v	>gi|693759|upncbi873 SecA homolog [
>generic|frv2_86382|Pisum_sativum_v	>gi|737595|upncbi778 H protein
>generic|frv2_86433|Pisum_sativum_v	>gi|738926|upncbi790 Phe ammonia ly
>generic|frv2_86521|Pisum_sativum_v	>gi|7414433|upncbi1628 beta-1,3 glu
>generic|frv2_86523|Pisum_sativum_v	>gi|75303233|upncbi2185 RecName: Fu
>generic|frv2_86824|Pisum_sativum_v	>gi|799369|upncbi844 metalloendopep
>generic|frv2_86933|Pisum_sativum_v	>gi|8489806|upncbi958 chloroplast p
>generic|frv2_87013|Pisum_sativum_v	>sp|ALDOARABIT|con106 contami-nant10
>generic|frv2_87264|Pisum_sativum_v	>sp|CAS1BOVIN|con3 contaminant3
>generic|frv2_87457|Pisum_sativum_v	>sp|CATDHUMAN|con62 contami-nant62
>generic|frv2_87529|Pisum_sativum_v	>sp|CTRABOVIN|con7 contaminant7
>generic|frv2_87602|Pisum_sativum_v	>sp|HBBHUMAN|con74 contaminant74
>generic|frv2_87968|Pisum_sativum_v	>sp|K1C15SHEEP|con10 contaminant10
>generic|frv2_88422|Pisum_sativum_v	>sp|K22EHUMAN|con23 contaminant23
>generic|frv2_88909|Pisum_sativum_v	>up|M7ZFL9|upncbi749 Photosystem II
>generic|frv2_89244|Pisum_sativum_v	>up|P20359|upncbi44 Actin, gamma n=
>generic|frv2_89366|Pisum_sativum_v	>generic|frv2_100460|p.sativum_wa1_
>generic|frv2_89831|Pisum_sativum_v	>generic|frv2_100707|p.sativum_wa1_
>generic|frv2_89838|Pisum_sativum_v	>generic|frv2_101690|p.sativum_wa1_

>generic|frv2_89899|Pisum_sativum_v
>generic|frv2_89921|Pisum_sativum_v
>generic|frv2_90358|Pisum_sativum_v
>generic|frv2_90594|Pisum_sativum_v
>generic|frv2_90642|Pisum_sativum_v
>generic|frv2_90741|Pisum_sativum_v
>generic|frv2_90830|Pisum_sativum_v
>generic|frv2_9250|franssen_5397_5
>generic|frv2_93350|FG536654_3
hypo
>generic|frv2_93581|FG528920_3
unna
>generic|frv2_93763|GH719756_5
ATFP
>generic|frv2_93827|GH719250_6
unch
>generic|frv2_95379|p.sativum_wa1_c
>generic|frv2_95597|p.sativum_wa1_c
>generic|frv2_95667|p.sativum_wa1_c
>generic|frv2_95685|p.sativum_wa1_c
>generic|frv2_95785|p.sativum_wa1_c
>generic|frv2_95787|p.sativum_wa1_c
>generic|frv2_95873|p.sativum_wa1_c
>generic|frv2_96292|p.sativum_wa1_c
>generic|frv2_96306|p.sativum_wa1_c
>generic|frv2_96500|p.sativum_wa1_c
>generic|frv2_96705|p.sativum_wa1_c
>generic|frv2_96977|p.sativum_wa1_c
>generic|frv2_97106|p.sativum_wa1_c
>generic|frv2_97108|p.sativum_wa1_c
>generic|frv2_97268|p.sativum_wa1_c
>generic|frv2_97451|p.sativum_wa1_c
>generic|frv2_97568|p.sativum_wa1_c
>generic|frv2_97597|p.sativum_wa1_c
>generic|frv2_97800|p.sativum_wa1_c
>generic|frv2_98054|p.sativum_wa1_c
>generic|frv2_98144|p.sativum_wa1_c
>generic|frv2_98184|p.sativum_wa1_c
>generic|frv2_98815|p.sativum_wa1_c
>generic|frv2_98818|p.sativum_wa1_c
>generic|frv2_99475|p.sativum_wa1_c
>generic|frv2_99547|p.sativum_wa1_c
>generic|frv2_99682|p.sativum_wa1_c
>generic|mut01|p.sativum_wa1_contig
>generic|mut03|contig21342_m
[MePr_
>generic|mut15|Contig2180_m
[MePr_D
>gene-
ric|mut44|Pisum_sativum_v2_Con
>generic|frv2_102293|p.sativum_wa1_
>generic|frv2_102446|p.sativum_wa1_
>generic|frv2_103908|p.sativum_wa1_
>generic|frv2_107353|p.sativum_wa1_
>generic|frv2_109970|p.sativum_wa1_
>generic|frv2_110796|p.sativum_wa1_
>generic|frv2_110900|p.sativum_wa1_
>generic|frv2_111175|p.sativum_wa1_
>generic|frv2_111243|p.sativum_wa1_
>generic|frv2_111308|p.sativum_wa1_
>generic|frv2_112129|p.sativum_wa1_
>generic|frv2_112323|p.sativum_wa1_
>generic|frv2_112607|p.sativum_wa1_
>generic|frv2_11295|franssen_6613_1
>generic|frv2_113035|p.sativum_wa1_
>generic|frv2_113427|p.sativum_wa1_
>generic|frv2_113709|p.sativum_wa1_
>generic|frv2_114489|p.sativum_wa1_
>generic|frv2_116233|p.sativum_wa1_
>generic|frv2_116847|p.sativum_wa1_
>generic|frv2_117139|p.sativum_wa1_
>generic|frv2_118048|p.sativum_wa1_
>generic|frv2_118750|p.sativum_wa1_
>generic|frv2_119032|p.sativum_wa1_
>generic|frv2_119206|p.sativum_wa1_
>generic|frv2_11987|franssen_7021_1
>generic|frv2_119963|p.sativum_wa1_
>generic|frv2_121222|p.sativum_wa1_
>generic|frv2_12183|franssen_7144_1
>generic|frv2_121992|p.sativum_wa1_
>generic|frv2_122363|p.sativum_wa1_
>generic|frv2_122549|p.sativum_wa1_
>generic|frv2_122906|p.sativum_wa1_
>generic|frv2_123630|p.sativum_wa1_
>generic|frv2_124736|p.sativum_wa1_
>generic|frv2_128958|p.sativum_wa1_
>generic|frv2_129361|p.sativum_wa1_
>generic|frv2_131292|p.sativum_wa1_
>generic|frv2_134153|p.sativum_wa1_
>generic|frv2_134997|p.sativum_wa1_
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>generic|frv2_15745|franssen_9262_1
>generic|frv2_16437|franssen_9673_6

>gi|1173069|upncbi1946 RecName: Ful	>generic|frv2_17472|franssen_10304_
>gi|1173198|upncbi2047 RecName: Ful	>generic|frv2_18031|franssen_10627_
>gi|120658|upncbi1949 RecName: Full	>generic|frv2_24576|franssen_14548_
>gi|120663|upncbi1950 RecName: Full	>generic|frv2_27405|franssen_16126_
>gi|121083|upncbi2005 RecName: Full	>generic|frv2_28827|franssen_16954_
>gi|121953|upncbi1931 RecName: Full	>generic|frv2_30684|franssen_17999_
>gi|12229958|upncbi2218 RecName: Fu	>generic|frv2_34066|franssen_20167_
>gi|12585295|upncbi2203 RecName: Fu	>generic|frv2_36233|franssen_21831_
>gi|12585296|upncbi2204 RecName: Fu	>generic|frv2_37128|franssen_22340_
>gi|131384|upncbi1957 RecName: Full	>generic|frv2_37919|franssen_22871_
>gi|133829|upncbi1969 RecName: Full	>generic|frv2_39563|franssen_23881_
>gi|1346673|upncbi2049 RecName: Ful	>generic|frv2_40402|franssen_24597_
>gi|13540393|upncbi980 histone H1,	>generic|frv2_40667|franssen_24765_
>gi|13591616|upncbi1425 UDP-D-glucu	>generic|frv2_41680|franssen_25444_
>gi|137582|upncbi1955 RecName: Full	>generic|frv2_42869|franssen_26248_
>gi|15594012|upncbi1653 putative th	>generic|frv2_48653|franssen_29885_
>gi|156530455|upncbi1190 ribosomal	>generic|frv2_49308|franssen_30322_
>gi|1706282|upncbi1953 RecName: Ful	>generic|frv2_50066|franssen_30848_
>gi|17367341|upncbi2162 RecName: Fu	>generic|frv2_50189|franssen_30935_
>gi|20138099|upncbi1891 RecName: Fu	>generic|frv2_50250|franssen_30978_
>gi|227247876|upncbi1720 unnamed pr	>generic|frv2_51174|franssen_31635_
>gi|232244|upncbi2019 RecName: Full	>generic|frv2_51878|franssen_32106_
>gi|2507443|upncbi2059 RecName: Ful	>generic|frv2_52065|franssen_32239_
>gi|25091388|upncbi2141 RecName: Fu	>generic|frv2_52101|franssen_32268_
>gi|257664820|upncbi1754 unnamed pr	>generic|frv2_52374|franssen_32449_
>gi|266742|upncbi2112 RecName: Full	>generic|frv2_52650|franssen_32630_
>gi|267076|upncbi2018 RecName: Full	>generic|frv2_52911|franssen_32818_
>gi|27466894|upncbi1020 thioredoxin	>generic|frv2_53245|franssen_33039_
>gi|295136979|upncbi2240 ATP syn-tha	>generic|frv2_53418|franssen_33161_
>gi|295137030|upncbi2291 photosyste	>generic|frv2_53742|franssen_33373_
>gi|295137041|upncbi2302 ribosomal	>generic|frv2_53890|franssen_33464_
>gi|295137044|upncbi2305 ribosomal	>generic|frv2_54037|franssen_33562_
>gi|296511935|upncbi1806 unnamed pr	>generic|frv2_54518|franssen_33874_
>gi|37051105|upncbi1449 glutathione	>generic|frv2_54824|franssen_34073_
>gi|400923|upncbi2024 RecName: Full	>generic|frv2_55115|franssen_34258_
>gi|436424|upncbi1560 HMG 1 protein	>generic|frv2_55219|franssen_34325_
>gi|462138|upncbi2030 RecName: Full	>generic|frv2_55445|franssen_34476_
>gi|46237494|upncbi1675 histone H1	>generic|frv2_55602|franssen_34581_

>gi|462579|upncbi1993 RecName: Full
>gi|62901479|upncbi2207 RecName: Fu
>gi|6730306|upncbi779 Chain D, C153
>gi|7339551|upncbi1626 convicilin [
>gi|75102455|upncbi2144 RecName: Fu
>gi|75219328|upncbi1893 RecName: Fu
>gi|75266203|upncbi2206 RecName: Fu
>sp|ALBUBOVIN|con1 contaminant1
>sp|CASBBOVIN|con5 contaminant5
>up|Q5DJ04|upncbi588 Chaperone prot
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>generic|frv2_59719|franssen_37082_
>generic|frv2_60085|franssen_37325_
>generic|frv2_60154|franssen_37372_
>generic|frv2_61484|franssen_38151_
>generic|frv2_61709|franssen_38283_
>generic|frv2_62734|franssen_38894_
>generic|frv2_6378|franssen_3713_4
>generic|frv2_642|franssen_366_2 De
>generic|frv2_66779|franssen_41226_
>generic|frv2_68228|franssen_42067_
>generic|frv2_69214|franssen_42687_
>generic|frv2_69335|franssen_42772_
>generic|frv2_69900|franssen_43151_
>generic|frv2_71160|franssen_43995_
>generic|frv2_71345|franssen_44107_
>generic|frv2_7183|franssen_4181_6
>generic|frv2_72274|franssen_44737_
>generic|frv2_7236|franssen_4212_5
>generic|frv2_73186|franssen_45330_
>generic|frv2_73814|Pisum_sativum_v
>generic|frv2_74395|Pisum_sativum_v
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>generic|frv2_77583|Pisum_sativum_v
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>generic|frv2_81319|Pisum_sativum_v
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>generic|frv2_8664|franssen_5052_2
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>generic|frv2_9662|franssen_5644_1
>generic|frv2_96934|p.sativum_wa1_c
>generic|frv2_97455|p.sativum_wa1_c
>generic|frv2_97667|p.sativum_wa1_c
>generic|frv2_97833|p.sativum_wa1_c
>generic|frv2_98820|p.sativum_wa1_c
>generic|frv2_98865|p.sativum_wa1_c
>generic|frv2_99156|p.sativum_wa1_c
>generic|frv2_99311|p.sativum_wa1_c
>generic|frv2_99334|p.sativum_wa1_c
>gi|1174592|upncbi2044 RecName: Ful
>gi|121053772|upncbi1165 putative v
>gi|126161|upncbi1962 RecName: Full

>gi|167047943|upncbi1210 ornithine

>gi|254797437|upncbi1245 chloroplas

>gi|2765097|upncbi1578 P54 protein

>gi|295137034|upncbi2295 cytochrome

>gi|295137042|upncbi2303 ribosomal

>gi|295137046|upncbi2307 ribosomal

>gi|461501|upncbi2114 RecName: Full

>gi|49175783|upncbi1080 ubiquitin a

>gi|62287174|upncbi2174 RecName: Fu

>gi|62909955|upncbi1470 peroxidase

>gi|75102461|upncbi2147 RecName: Fu
>sp|ALBUHUMAN|con54 contaminant54

>sp|CASKBOVIN|con6 contaminant6
>sp|GSTP1HUMAN|con72 contaminant72