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Toward a PA-Inhibitor Complex Crystal System: Influenza Polymerase Acidic Protein Fusion Constructs and Protein Expression

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Abstract

Globally, three to five million people are afflicted on a yearly basis with serious illnesses due to influenza. In attempts to combat this epidemic, vaccines and antivirals are developed, yet they are not effective enough. The polymerase acidic protein (PA) is vital for viral replication, and inhibiting PA would potentially stop the virus from replicating. In order to inhibit PA effectively, the structure of the protein inhibition site is beneficial but has not yet been obtained because the site is blocked by another protein in crystal structures. Our solution is to fuse different proteins to PA to open up the structure to allow visualization of PA-inhibitor complexes. Various molecular biology techniques were used to create 18 different DNA constructs that were then transformed into bacterial cell lines to be expressed as protein.

Acknowledgements

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Chapter 1: Introduction

1.1 Problem

The effects of influenza are detrimental to human health and can even culminate in death. Influenza affects 5-20 percent of the population every year in the United States (3). Though the influenza virus generally affects the upper respiratory systems and the symptoms are mild, serious complications can arise. The consequences can be as serious as resulting in death; US yearly mortality rates can range from 3,000 to 49,000 (3). The World Health Organization estimates that there are 290,000 to 650,000 global deaths and three million to five million serious illnesses a year are due to influenza (25).

The two medical defenses against influenza are vaccines and antiviral therapeutics. Vaccines train the immune system to recognize viruses to have a quicker and more effective immune response by introducing antigens of the viruses. The introduction of these antigens spurs the development of specific antibodies. Two antigens that are glycoproteins are often used; these are hemagglutinin (HA), which enables the viral nucleic acids to enter into the cell, and neuraminidase (NA), which has many functions, one of which is to prevent aggregation of viruses on the cell surface. The antivirals available are NA inhibitors, polymerase acidic endonuclease inhibitors, and M2 ion channel inhibitors. The NA inhibitors are oseltamivir phosphate (Tamiflu), inhaled zanamivir (Relenza), and intravenous peramivir (Rapivab), and function by allowing the aggregation of viruses on a cell surface. The most common influenza treatment, oseltamivir, only shortens the duration of symptoms by 0.7-1.5% with a clinical efficacy of 60-70% (17). The polymerase acidic endonuclease inhibitor is oral baloxavir marboxil (Xofluza) which interrupts transcription and prevents replication.

The M2 ion channel inhibitors, amantadine and rimantadine, have incurred very high resistance in viruses, so they are not recommended for use (1). Currently, NA inhibitors have low resistance, however this could change. Baloxavir has had less success with "variants with reduced susceptibility emerging frequently during monotherapy" (1). Just as resistance to M2 ion channel inhibitors has developed, resistance to other antivirals could happen, especially since HA and NA are under selective pressure to mutate to develop resistance. Over time, antigenic variations result in the development of antigens that are not recognized by antivirals.

The accumulation of mutations can result in ineffective antivirals and vaccines since the glycoproteins are modified enough that the specific antibodies do not recognize the antigens. The increased use of these treatments has been known to increase the likelihood of resistance to develop, just as the overuse of antibiotics contributes to antibiotic resistance. Since NA and HA are both surface proteins they are more likely to evolve at a quicker rate than cytosolic, internal proteins (26). Since viruses have high reproduction rates, they can mutate surface proteins that are targeted by vaccines, rendering the vaccines ineffective. However, an oral therapeutic targeting an internal protein within the virus that does not mutate quickly could provide a solution to this. A protein that is well conserved across influenza strains would be the most desirable therapeutic target, since it would have efficacy for multiple strains of influenza for a number of years.

In figure 1, it can be seen that NA (left) has a very high mutation rate, while polymerase acidic (right) protein (PA) has a much lower rate of mutation and is highly

conserved, especially surrounding the green protein in the center, which is the site of interest.

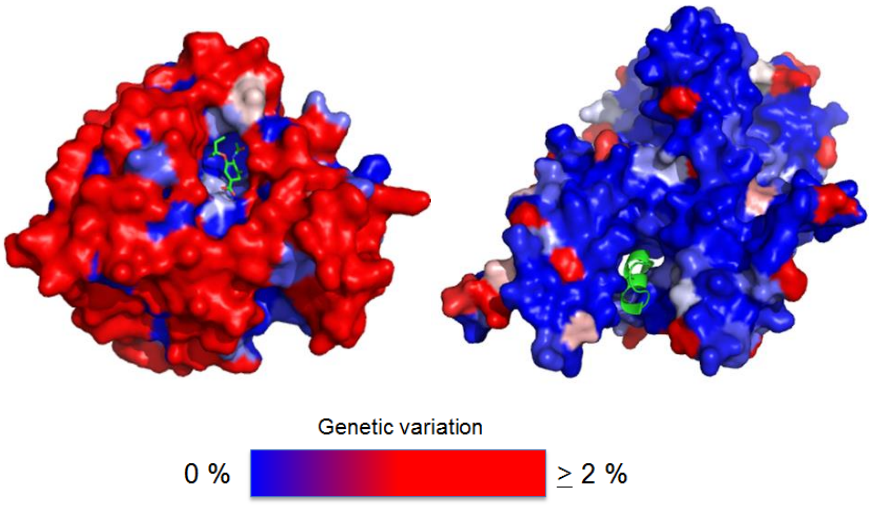

Figure 1 Higher genetic variation in neuraminidase (left) than polymerase acidic (right). The color scale represents the degree of genetic variation in the proteins with red being greater than or equal to 2% and blue being 0% genetic variation.

Polymerase acidic is a part of the RNA-dependent RNA polymerase (RdRp) heterotrimer, which is well conserved because it is responsible for the transcription or replication of the virus. The three subunits within the RdRp heterotrimer consists of polymerase A (PA), polymerase basic 1 (PB1), and polymerase basic 2 (PB2). Figure 2 provides a structure of the RdRp complex from the article in *Nature* "Crystal structure of the polymerase PAC–PB1N complex from an avian influenza H5N1 virus" (10).

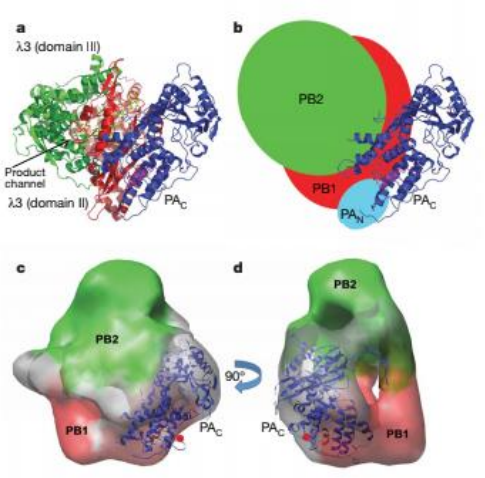

Figure 2 Structure of RdRp heterotrimer from Xiaojing He and Jie Zhou and colleagues. The figure demonstrates the structure of the protein complex (10).

Polymerase and endonuclease activity is carried out by PB1, while cap binding is a function of PB2 (10). Even though the exact functions are not known, PA is required for viral replication, if only for the purpose of providing support for the heterotrimer. It bridges PB1 and PB2 and is thereby involved in replication of the viral RNA (10).

As can be seen in figure 3 from "The structural basis for an essential subunit interaction in influenza virus RNA polymerase", the carboxy terminus of PA forms a pocket in which PB1 binds. The interaction of PA with the N-terminal tip of PB1 is small compared to the size of the 250 kDa complex, but it is very important for the function of the complex, so it is completely conserved (26)(12). Any mutation in PB1 that rendered it unable to bind to PA resulted in impaired replication of the virus (25).So likely PA and PB1 could not tolerate individual mutations in this region due to selective pressure. Indeed, it was found that there must be mutations in both PA and PB1 for resistance to develop, unlike the M2 or NA inhibitors, in which one mutation can result in resistance (14). Targeting protein-protein interactions is a strategy to inhibit viral activity, since

these interactions are vital to viral functioning (24). Disruption of PA and PB1 binding prevents viral replication, implying PA binding-molecules that inhibit RdRp may serve as influenza therapeutics (29).

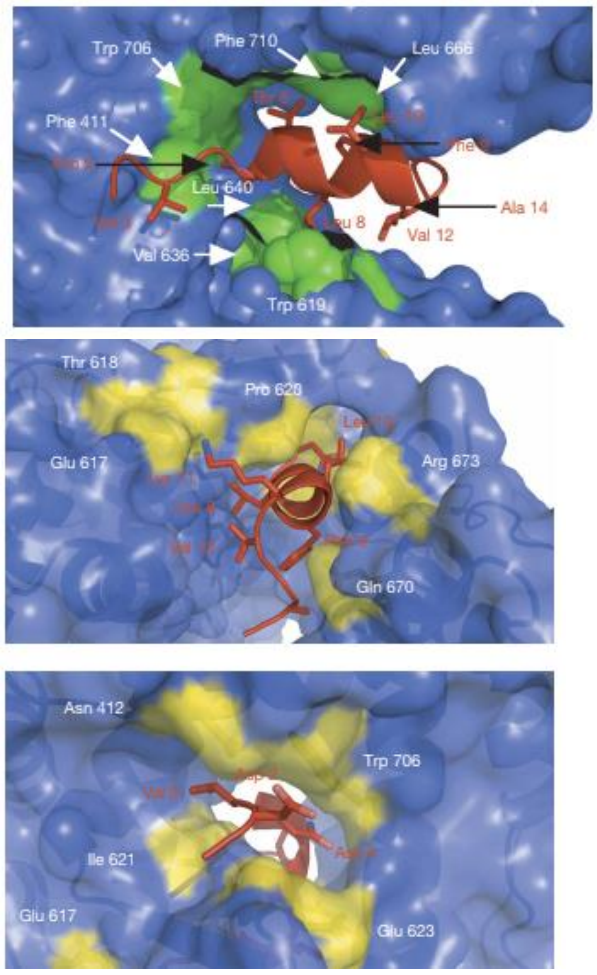

Figure 3 The hydrophobic interactions of PA and PB1 (left) and the hydrogen bonds between the proteins (right). Images were obtained from Obayashi in: "The structural basis for an essential subunit interaction in influenza virus RNA polymerase"(23).

It would seem that PA would be a very desirable therapeutic target because of its importance in viral replication in the RdRp heterotrimer, its low mutation rate, and its distinct role in providing the structural polypeptide backbone for RdRp.

Others have developed small molecules that bind the pocket of PA that interacts with PB1 (9), which does inhibit RdRp activity, but these molecules currently have too low of affinity to be useful therapeutic inhibitors. Serena Massari, et al, from the Univeristy of Perugia extensively reviewed the current progress in finding inhibitors for PA and summarized their findings by saying:

> *Although there have been considerable advances in the potency of PA−PB1 heterodimerization inhibitors, further efforts are required in order to improve the potency of these compounds to the nanomolar range as well as their ADME profile, especially with regard to solubility. Overall, the inhibitors described here are still very far from being considered lead candidates. Although the most interesting inhibitors are nontoxic, they are not potent enough and do not possess proper drug-like properties (14).*

Protein structure is frequently used to guide drug development efforts. We therefore believe more structures of PA bound to current inhibitors could facilitate the discovery of inhibitors with higher affinity for binding the site of interest. Unfortunately, current crystal structures of the PB1 binding site of PA (figure 4a) are occluded by a loop of an adjacent PA (figure 4b) by crystal packing. Therefore, the existing apo (free of small molecules) PA crystal structures cannot be utilized to discover inhibitors because their crystal packing makes the inhibitor binding site virtually inaccessible (15).

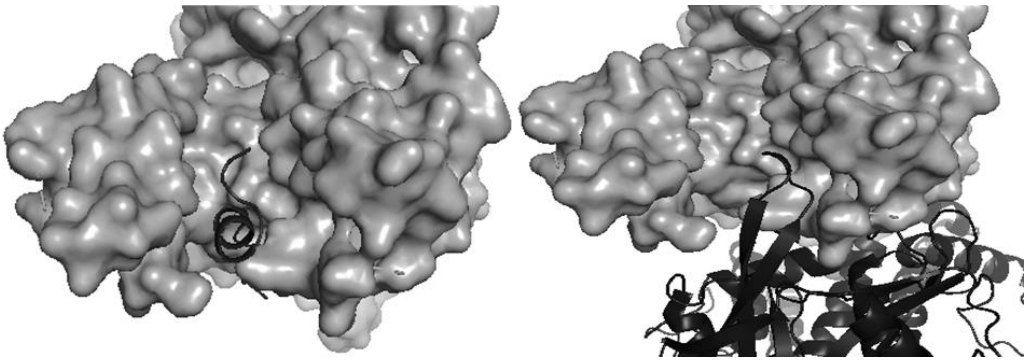

Figure 4 a (left) Interaction of PA with PB1 peptide. PA is rendered as surface and the PB1 peptide (PDB ID: 2ZNL) as a cartoon to visualize the PA binding pocket.

Figure 5 b (right) apo-PA crystal packing. PA (PDB ID: 4IUJ) is rendered as a surface, and a loop from an adjacent molecule of PA (cartoon) occludes the PB1-binding site and desired inhibitor-binding site.

In order to create an apo PA crystal system with no loop occluding the site of interest, our approach is to create different protein fusions of PA that will alter the crystal packing structure of PA, which could allow the visualization of the apo protein through x-ray crystallography. The overall process to accomplish this feat involves vector design, vector construction, small scale protein test expression and purification, large scale protein expression, protein crystallography and x-ray diffraction, and collaboration for iterative inhibitor improvement.

To match previously published research, we are using the PA protein (Appendix C) from the Wilson-Smith 1933 H1N1 strain, and specifically the portion of the protein that binds PB1, residue numbers 254-716. The objective of the first step of the project was to create plasmids with PA inserts ligated adjacent to various DNA sequences that will express different fusion proteins, like green fluorescent protein (GFP), maltose binding protein (MBP), glutathione S-transferase (GST), trigger factor (TF), thioredoxin (Trx) and small ubiquitin-like modifier protein (SUMO). See Appendix C for the DNA insert sequences of these proteins. These proteins were selected to create protein fusions

with PA since they are commonly used proteins that typically express and purify well, and have been successfully crystallized. We also designed an internal loop deletion of PA (PAt) that removes a disordered loop near the PB1 binding site, truncation: 373-391. Fusion of these 7 proteins to the C-terminus of PA and PAt along with free C-termini creates a set of 16 expression plasmids.

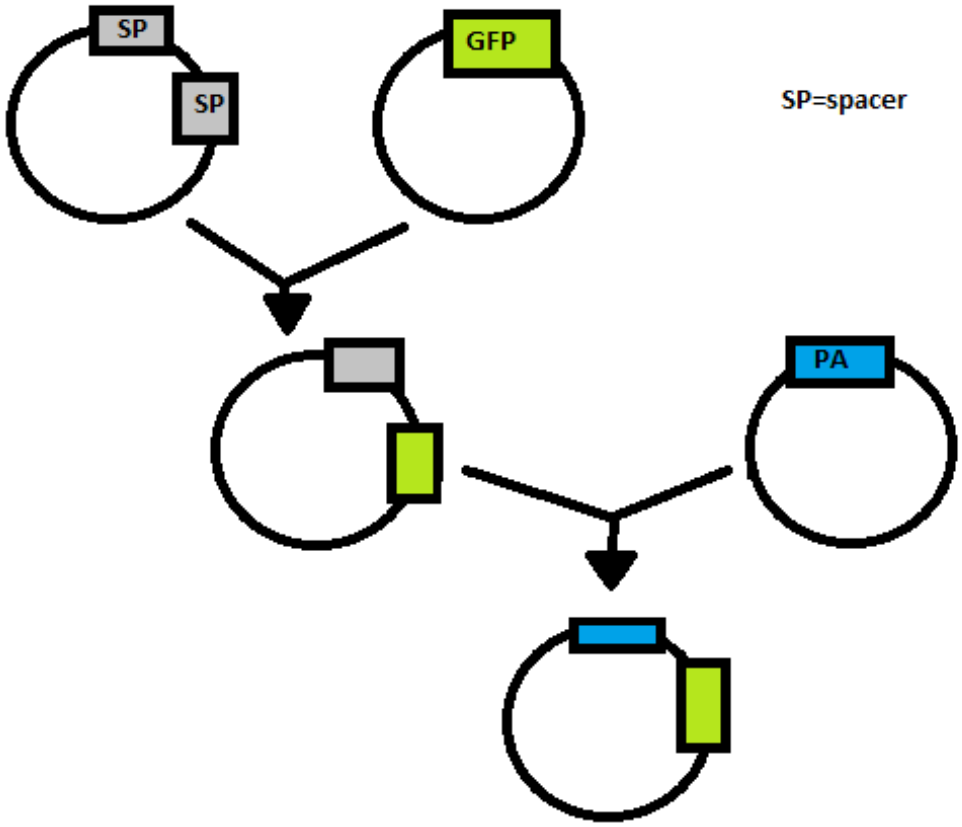

Figure 5 A schematic of the construction of vectors. GFP is used as a representative of the 7 different protein. GFP was digested, PCR-ed, and then ligated into the empty vector. The PA gene was then digested and ligated into the toolbox vector. The color of the rectangles is used to represent the different DNA sequences of proteins. SP is a spacer or DNA sequence.

This thesis describes construction of these expression vectors and initial test expressions in *E. coli*. After successful large-scale test expression, these proteins will be purified, which will allow only the proteins of interest to be carried through the next step in a pure form. Lastly, the purified proteins would be screened for conditions under which they crystallized. Ultimately, crystal structures of apo PA could be used to identify potential therapeutic inhibitors that would be used in influenza therapeutics to prevent the replication of the virus.

Chapter 2: Methods

2.1 Plasmid Design

Taylor Balk and Dr. Daniels began the project with literature searching and vector design in Snapgene. They decided to append the fusions to PA (Appendix C) at the C-terminus since the crystal packing structures were more likely to disrupt the occlusion of the site of interest. The proteins that were to be fused were chosen because they are commonly used and are known to express well. They are also known to have solubilizing properties. The protein loop of PA that occludes the PB1-binding site of adjacent PA's was also truncated off with the Pat version of every vector.

2.2 Construction of DNA Toolbox Vectors

The following methods are the generalized protocols used to engineer plasmids containing the protein fusions and ready to receive PA by golden gate cloning. Each protocol was performed 8 times to construct the 8 toolbox vectors, which is the fusion protein ligated into the BL-21 derivative vector.

2.2.1 Polymerase Chain Reactions to Amplify Inserts

Primers were designed to amplify the fusion proteins from existing vectors (courtesy of C. Garvie, Broad Institute, see Appendix A). See appendix B for primer sequences. The temperature used for the annealing step was determined using the NEB Tm calculator. The annealing temperature was 5C under the lowest primer Tm. For example, GFP-F had the tm 60/76 (initial match/later cycle match). GFP-R had the tm of 52/62. the temperature for the annealing steps was decided to be 47C for the first 10 cycles, and 57C for the last 20 cycles.

PCR							
Vector	**GFP**	**MBP**	**GFPa**	**GST**	**TF**	**Trx**	**SUMO**
Tm	47/57	51/66	44/55	58/66	55/66	55/66	55/66

The forward and reverse primers were diluted to 10 uM solutions and the template DNA of toolbox vectors was also diluted. The following was pipetted to mix in a PCR tube:

1. 35 ul MB water
2. 10 ul 5X OneTaq Standard Reaction Buffer
3. 1 ul 10 uM forward Primer
4. 1 ul 10 uM reverse Primer
5. 1 ul 10 mM dNTPs
6. 1 ul of 1ng/ul Template DNA (vectors)
7. 0.25 ul OneTaq Hot Start DNA Polymerase

The thermocycler was set to the annealing temp based on the T M's determined in the first step.

An example is provided below:

Initial denaturation:
94°C 30 seconds
10 cycles:
94°C 30 seconds
47°C 60 seconds
68°C 1 minute per kb

20 cycles:
94°C 30 seconds
57°C 60 seconds
68°C 1 minute per kb

Final extension:
68°C 5 minutes
Hold: 4–10°C

Following PCR amplification, a QIAquick PCR Purification Kit was used to purify the inserts. To begin, 5 volumes of Buffer PB were added to 1 volume of the PCR sample. If the color was orange, then 10ul of 3M pH 5 sodium acetate* was added to the mixture, turning the solution yellow.

*the sodium acetate solution was made by adding 12.3 g of sodium acetate to water, titrating it to a pH of 5 by adding glacial acetic acid.

A QIAquick spin column was placed in a provided 2 ml collection tube. The DNA was bound by applying the sample to the QIAquick column and centrifuging for 30–60 s. The flow-through was discarded. The DNA was washed with 0.75 ml Buffer PE, then was centrifuged for 30–60 and then centrifuged again for an additional 1 min. To elute the DNA, the column was placed in a clean microcentrifuge tube and 50 µl Buffer EB (10 mM Tris·Cl, pH 8.5) was pipetted into the center of the QIAquick membrane and let sit for one minute, then the column was centrifuged for 1 min.

2.2.2 Restriction Enzyme Double Digestion and Diagnostic Gel with Optimized Protocol to Omit Gel Purification

Normally, after PCR or digestions, the DNA must be isolated and purified by agarose gel electrophoresis and then extracted from the gel. This procedure is costly timewise. In attempts to cut back on time, this step was omitted by using CIP and DPNI. CIP is used when excising portions of the vector backbone because it ensures that the 5’ end of removed fragment will not re-ligate into a plasmid. DPN1 digests methylated DNA (only bacterial DNA is methylated). Therefore, DPNI treatment removes any plasmid template remaining from PCR amplification. For the double digestion, appropriate restriction enzymes should be used for the specific vectors. The following is the components of the solutions used in one digestion of a PCR insert:

Double Digest								
	GFP	**MBP**	**GFPa**	**GST**	**TF**	**Trx**	**SUMO**	**DLP002**
Nucleas e-free water	23 µl	3 µl	3 µl	3 µl	1 µl	1 µl	1 µl	26 µl
10X CutS	5 µl	6 µl	6 µl	6 µl	6 µl	6 µl	6 µl	5 µl
NheI	1.5 µl	1 µl	1 µl	1 µl	1 µl	1 µl	1 µl	1 µl
XhoI	1.5 µl	1 µl	1 µl	1 µl	1 µl	1 µl	1 µl	1 µl
Quick CIP	0 µl	0 µl	0 µl	0 µl	0 µl	0 µl	0 µl	2 µl
DPN1	0 µl	1 µl	1 µl	1 µl	1 µl	1 µl	1 µl	0 µl
DNA	19 µL (80 ng/µL)	48 µl (124 ng/µl)	45 µl (58.4 ng/µl)	48 µl (76 ng/µl)	50 µl (98.6 ng/µl)	50 µl (16.8 ng/µl)	50 µl (41.3 ng/µl)	15 µl (33 ng/µL)

After being mixed, the tubes were placed in the Isotemp to incubate for 60 mins at 37C. Enzymes were then heat inactivated for 20 minutes at 80C. To ensure that the DNA was cut in the correct location by visualizing DNA of the appropriate length, a diagnostic gel was run. Since gels are made in various different ways, the following is the methods used to create 0.8% agarose gels. 1.6 g of agarose and 200 ml TAE1x were combined, and 20 ul of gel loading dye purple (6x) from NEB was added. Then 5 ul of digested and undigested DNA were mixed with 1 ul of gel loading dye purple (6x) and pipetted into the gel after the 1x TAE was poured in the trap. The undigested DNA is included for comparison. Gels were run at 120V for 30-45 mins.

2.2.3 Ligation

To determine the concentration of the vector and insert, the absorbance was determined using A260 from either a Nanodrop or microplate reader in the student biochemistry lab. The following reaction components were set up in a microcentrifuge tube on ice, in the following order: 1) water 2) T4 DNA Ligase Buffer 3) Insert DNA 4) Vector DNA 5) T4 DNA ligase

COMPONENT	20 µl REACTION							
	GFP	NoFusion	MBP	GFPa	GST	TF	Trx	SUMO
T4 DNA Ligase Bµffer (10X)	2 µl	2 µl	2 µl	2 µl	2 µl	2 µl	2 µl	2 µl
Vector DNA- DLP2 cut w/ NheI/XhoI	8 µl (50 ng)	0.30 µl (50 ng)	0.30 µl (50 ng)	0.30 µl (50 ng)	0.30 µl (50 ng)	1 µl (167ng)	1 µl (167ng)	1 µl (167ng)
Insert DNA cut w/ NheI/XhoI	1µl (24 ng)	1.0 µl	0.25 µl (31.1 ng)	0.32 µl (18.8 ng)	0.25 µl (19 ng)	1µl (100 ng)	2µl (32ng)	1µl (35 ng)
Nuclease-free water	8 µl	15.7 µl	16.7 µl	16.4 µl	16.5 µl	15 µl	14 µl	15µl
T4 DNA Ligase	1 µl	1 µl	1 µl	1 µl	1 µl	1 µl	1 µl	1 µl

*vector concentration is estimated expecting 50% recovery from DNA put into the double digest. Ratio of insert:vector (760bp:5.8kb) is then 3:1 or 4:1. NEB ligation calculator was used.

The reaction was gently mixed by pipetting up and down. Since the restriction enzymes used produced cohesive (sticky) ends, the reaction was incubated at room temperature for 60 minutes. Then it was heat inactivated at 65°C for 10 minutes, and stored in the -20C.

2.2.4 Transformation, Purification, and Glycerol Stock Creation

2.2.4.1 Transformation

For C2987I: A tube of NEB 5-alpha Competent *E. coli* cells was thawed on ice until the last ice crystals disappeared. 50 µl (varied amounts of cells based on the expectations of successful transformation, I.e. if it was expected to be successful could use as little as 8ul of cells) of cells were mixed gently and carefully pipetted into a transformation tube on ice. 1-5 µl containing 100 ng of plasmid DNA were added to the cell mixture. The tube was inverted 4-5 times to mix cells and DNA. It was important not to vortex as that could lyse cells. The mixture was placed on ice for 30 minutes. The solutions were heat shocked at exactly 42°C for exactly 30 seconds, then placed on ice for 5 minutes. 950 µl of room temperature SOC was pipetted into the mixture. The solutions were placed at 37°C for 60 minutes in the shaker at 250rpm. The cells were mixed thoroughly by flicking the tube and inverting. 50 µl of each solution were spread onto a selection plate, which was then incubated overnight at 37°C. There is the option to incubate at 30°C for 24-36 hours or 25°C for 48 hours, but leaving plates on the bench always resulted in very slow growth of colonies, so much so that the plates had to be transferred to an incubator.

2.2.4.2 Overnight Inoculation Glycerol Stock Creation

A single colony was swiped from the transformation plates and swirled in LB media with amp in test tubes using plastic inoculation loops for 16-hour outgrowth. The next morning, 300 µl of the overnight cultures and 300 µl of 50% glycerol (sf) were mixed and placed in the –80C.

2.2.4.3 DNA Purification

Following transformation and overnight outgrowth, the bacterial cells must be lysed to harvest the DNA that they amplified. This was conducted using a QIAprep Spin Miniprep Kit. The remaining overnight outgrowth was spun at 4150 rpm at 25C to pellet the bacterial cells. Next, the pelleted bacterial cells were resuspended in 250 µl Buffer P1 and transferred to a microcentrifuge tube. Then, 250 µl Buffer P2 were added and mixed thoroughly by inverting the tube 4–6 times. It was realized that it is important that P1 and P2 are swirled before addition since there are particulates that settle. Immediately after buffer P2 was added, 350 µl of Buffer N3 were added, and the solutions were mixed immediately and thoroughly by inverting the tubes 4–6 times. The solutions were then centrifuged for 10 min at 13,000 rpm (~17,900 x g) in a table-top microcentrifuge. The supernatant was applied to a QIAprep 2.0 spin column by pipetting, which was centrifuged for 30-60 s. Then it was washed by adding 0.5 ml Buffer PB and centrifuging for 30-60 seconds, then adding 0.75 ml Buffer PE and centrifuging again. In between each addition and centrifugation, the flow-through was discarded. After the buffer PB addition, centrifugation was repeated at full speed for an additional 1 min to remove residual wash buffer. The QIAprep 2.0 column was placed in a clean 1.5 ml microcentrifuge tube to elute the DNA into by pipetting 50 µl Buffer EB (10 mM Tris·Cl, pH 8.5) to the center of each QIAprep 2.0 spin column, letting it stand for 1 min, and centrifuging for 1 min.

2.3 Construction of PA-Fusion Vectors

2.3.1 Golden Gate Reaction

The golden gate assembly is a reaction in which both digestion and ligation occur within the same reaction tube. It streamlines the process and makes DNA construct engineering more efficient.

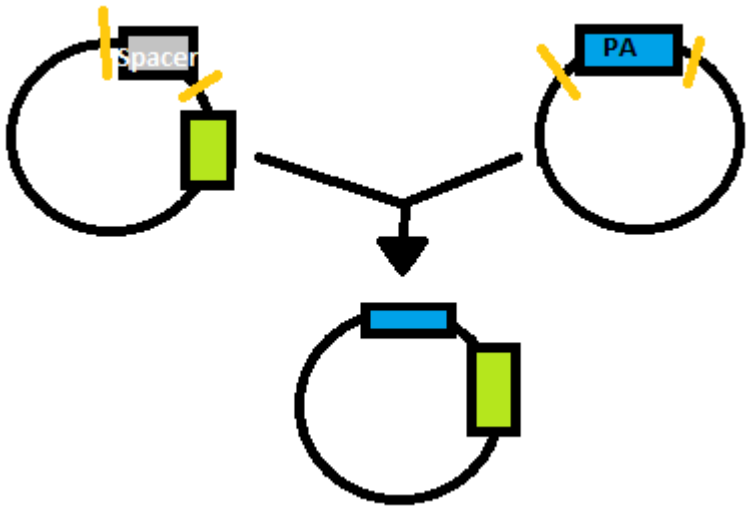

Figure 6 Golden gate reaction both digests a plasmid, then ligates the newly freed protein into a new plasmid. The grey rectangle represents a spacer DNA sequence, the blue PA, and the green any fusion protein. The orange lines represent restriction enzyme digestion sites, that when digested form sticky ends (overhanging single-stranded DNA sequences). The sticky ends of the protein sequence and the vector are combined with T4 ligase.

The following is the conditions of the 8 different reactions that were performed to construct the DNA fusions. The components below were mixed by pipetting up and down and were then centrifuged. The DNA sequences for the inserts can be found in Appendix C.

COMPONENT	GFP (182.6 ng/µl) (6528 bp)	NoFusion (222.3 ng/µl) (5790 bp)	MBP (111.68 ng/µl) (6500 bp)	GFPa (91.1 ng/µl) (6888 bp)	GST (175.5 ng/µl) (6453 bp)	TF (215 ng/µl) (7083 bp)	Trx (184 ng/µl) (6115 bp)	SUMO (212 ng/µl) (6081 bp)
MB water	15 µl	16.2 µl	15.7 µl	15.4 µl	16.0 µl	15.92 µl	15.8 µl	15.4 µl
T4 DNA Ligase Bµffer (10X)	2 µl	2 µl	2 µl	2 µl	2 µl	2 µl	2 µl	2 µl
PA (4126 bp) (92 ng/µl)	1.30 µl	0.24 µl	0.40 µl	0.52 µl	0.28 µl	0.48 µl	0.55 µl	0.55 µl
Plasmid	0.41 µl	0.34 µl	0.67 µl	0.82 µl	0.43 µl	0.35 µl	0.41 µl	0.35 µl
T4 DNA Ligase	0.5 µl	0.5 µl	0.5 µl	0.5 µl	0.5 µl	0.5 µl	0.5 µl	0.5 µl
BSaI-HFv2	0.75 µl	0.75 µl	0.75 µl	0.75 µl	0.75 µl	0.75 µl	0.75 µl	0.75 µl

After mixing, the tubes were incubated at 37C for one hour. Then, the tubes were placed in a 60C for 10 minutes to allow BsaI to achieve its highest activity, while T4 ligase is at a low activity. For the reactions, a 1:1 insert:vector ratio was used, with 75 ng of the starting plasmid being used. A sample calculation of DLP5 is shown:

75ng DLP5/222.3ng/ul = 0.34 ul 0.34ul DLP5/5790 DLP5 bp = x/4126 PA bp => x=0.24 ul PA

2.3.2 Transformation, Purification, and Glycerol Stock Creation

Following the Golden Gate reactions, the same protocols in subsection 2.2.5 were used for transformation, DNA purification, and glycerol stock creation.

2.4 Small Scale Expression

2.4.1 Expression Strain Transformations

Prior to expression, the vectors were transformed into *E. coli* expression strains. Five different strains were used, since it was believed different strains could possibly increase solubility.

2.4.1.1 NiCo

Two tubes of NiCo21(DE3) Competent E. coli cells were thawed on ice. Then 8.3 ul of cells were aliquoted into 10 tubes that were placed in ice. Plasmid DNA (1uL, ~100ng) were added to the cell mixture. The tubes were carefully flicked 4–5 times to mix cells and DNA. The mixture was placed on ice for 30 minutes, heat shocked at exactly 42°C for exactly 10 seconds, and placed on ice for 5 minutes. Room temperature SOC (950 µl) was added into the mixture, which was shaken at 250rpm at 37°C for 60 minutes. The selection plates were warmed to room temperature. The cells were mixed thoroughly by flicking the tube and inverting. Each dilution (100 µl) was spread onto a selection plate and incubated overnight at 37°C.

2.4.1.2 T7 Express, T7 Shuffle, and Tuner

For the transformation of T7 Express Competent *E. Coli* cells the same protocol for

NiCo21(DE3) cells was used except 33 µl of cells were used. The same protocol was used for T7 Express Shuffle Competent *E. Coli* cells Tuner cell too, the traditional 50 µl of cells were used.

2.4.1.3 Artic Express

https://www.agilent.com/cs/library/usermanuals/Public/230191.pdf

The competent cells were thawed on ice and gently mixed. For each expression plasmid transformation, 12ul of cells were aliquoted into the 8 tubes. XL10-Gold β-mercaptoethanol mix provided with this kit was diluted 1:40 with dH2O. Each 12-µl aliquot of cells required 1 µl of diluted β-mercaptoethanol. The contents of the tubes were swirled gently. The cells were incubated on ice for 10 minutes with gentle swirling every 2 minutes. The expression plasmid DNA (1 µl), containing the gene of interest, was added to each tube of cells and swirled gently. The reactions were incubated on ice for 25 minutes. SOC medium was preheated in a 42°C water bath for use in step 11. Each transformation reaction was heat shocked in a 42°C water bath for 20 seconds. The reactions were incubated on ice for 2 minutes. Preheated (42°C) SOC medium (200 µl) were added to each transformation reaction. The reactions were placed in a shaker at 37°C for 1 hour with shaking at 225–250 rpm. Using a sterile spreader, spread 25 µl of the cells transformed with the experimental DNA onto LB agar§ plates that contain the appropriate antibiotic for selection of the expression plasmid. The plates were then incubated overnight at 37°C. The overnight overgrowth in LB media must contain gentamycin, since the cells have a resistance gene for it.

2.4.2 Generalized/Optimized Expression Protocol

Small scale expression was a process of modification and reiteration. There were 18 different expressions run, so having every protocol listed would be tedious for the reader. Instead the “generalized” protocol will be listed along with a table provided with all the variations. Through analysis of the gels, it appeared that there were some specific conditions that improved

solubility, but in general, the optimal conditions ended up just being the original conditions attempted as most modifications did not make significant improvements.

Day 1

Sufficient media was made with the antibiotic ampicillin (1 µl/ml), for overnight growths. 2mL LB/Amp was added to 24-well plates or tubes. Each well was inoculated from frozen glycerol stock by taking a frozen stab of the vector construct in the selected expression strain. The plate or tubes were shaken at selected rpm at appropriate temperature. Generally, it was started at 5pm to allow for a 16-hour overnight outgrowth.

Day 2

Fresh media with ampicillin was inoculated from overnight starter cultures, 20 ul overnight culture into 2ml of fresh media (or corresponding 1:1000 dilution culture:media). Then the tubes or plates were placed back in the shaker. After 2 hours of outgrowth the OD600 reading was taken with an UV-Vis spectrophotometer. The rate of growth was determined by monitoring density of cells revealed by their density. Right before the cultures reached the selected induction density, they would be transferred to a different temperature. At the proper cell density, the cultures were induced with the selected concentration of IPTG. Then the cultures were incubated for the time required depending on the temperature they were incubating at. The cultures were spun down at 4000 rpm for 8-15 mins in an Eppendorf centrifuge (found in Dr. Biffinger's lab), forming pellets. Then the media was aspirated off and the cell pellets were placed in the -80C.

2.4.3 Bacterial Lysis

Pierce protease inhibitor mini tablet (1 tablet), EDTA-free (A32955) was dissolved in 10 mL Bugbuster. Then, the mix was warmed to room temperature, and DTT, the denaturing agent, was added. The previously frozen cell pellets were resuspended in 200 uL room temperature BugBuster Master Mix by pipetting. The cell suspension was incubated on nutator at a slow

setting for 10–20 min at room temperature. The Total Cell Lysate (20 µL) was removed for SDS PAGE analysis. Insoluble cell debris was removed by centrifugation at 16 kg for 20 min at 4°C.

2.4.4 Nickel Bead Purification

PureProteome Nickel Magnetic Beads were resuspended by vortexing. 20 µL of magnetic bead suspension (20 µL of suspension can bind 20–110 µg of His-tagged protein.) were aliquoted into either a 96-well plate or tubes, which was then placed on the magnetic base to collect the beads. Storage buffer was carefully removed with a pipette. The plate was removed from the magnetic base. The magnetic beads were resuspended in 200 µL of Wash Buffer (50 mm tris, 300 mm NaCl, 10 mm imidazole at pH 8) and incubated on the nutator for one minute at room temperature. The tube was placed back onto the magnetic stand for the beads to collect.

For SDS-PAGE analysis, 20uL of cleared cell lysate were isolated on a 96-well plate or into tubes. The wash buffer was removed from the beads. The plate was removed from the magnetic base. The remaining cleared cell lysate was moved to the plate containing Ni beads and was incubated on a nutator for 30 minutes at room temperature. The pellet was saved for SDS PAGE analysis. The plate was placed back onto the magnetic base and the beads were allowed to migrate to the magnet. The beads were captured, and lysate was removed. This PA-depleted lysate was saved in a 96-well plate or tubes for analysis. The magnetic beads were washed by incubating in 200 µL of Wash Buffer with gentle mixing for one minute at room temperature. For some experiments, the first wash in a 96-well plate was saved for analysis. The plate was placed back into the magnetic base and the beads migrated to the magnet. Wash Buffer was removed. The bound protein was eluted by adding 50 µL of Elution Buffer (50 mm tris, 300 mm NaCl, 300 mm imidazole at pH 8), incubating with gentle mixing for two minutes at room temperature, and placing the plate back into the magnetic base to separate and collect the eluted PA fraction into a clean 96-well plate.

2.4.5 SDS-PAGE Analysis

The Bio-Rad Mini-PROTEAN Precast gel 4-15% was prepared by opening gel bag, taking off the sticker on the bottom, and removing the comb from the wells. The electrophoresis rig was set up by putting the prepared gel in cartridge. The inner compartment of rig was filled with Novex Tris-Glycine SDS Running Buffer (10x) cat no. LC2675-5. After ensuring there was no leaking from the inner compartment, buffer was added to the fill line. An equal volume (eg. 10uL loading buffer to 10uL sample) of Tris-Glycine SDS Sample Loading Buffer (2x) novex LC2676 was added. Reducing agent (1/20th volume of 20x DTT) was added. The samples were heated for 3 min (90-95C), then stored at -20C and boiled again if the gel was not run immediately. The samples were spun down. At this point, could either run gel or save samples in -20C. The gel wells were flushed out by pipetting buffer into them. The samples and protein ladder (Precision Plus Dual Color Bio-Rad 1610374) were added to gel. The samples were electrophorized at 200V for 30-40 mins periodically checking to see if the buffer was covering the wells.

2.4.6 Modified Fractioning after Lysis for Analysis

The nickel bead purification step was not a necessary step of the protocol to determine if the protein fusion was soluble. So following lysis, the total cell lysate and clear cell lysate were fractioned off and then prepared for SDS-PAGE analysis.

2.5 Trigger Factor- PA Fusion Large Scale Expression and Analysis

2.5.1 Optimization of Conditions for Highest Solubility for Trigger Factor-PA Fusion

Since DLP22 had some amount of soluble protein it was used to be scaled up for FPLC purification. To find the best conditions for the highest solubility of the TF-PA fusion, different expressions were run on a gel again to compare with standardized gel variables. A Tuner cell strain expression at 16C (DLP33) with IPTG concentrations of 0.45 and 1.5mM, an Artic Express

expression at 16C and 0.1mM IPTG concentration, and a Shuffle expression at 16C and 1.0mM IPTG concentration were all run on a gel and compared. The NiCo expression at 37C and a 0.1mM IPTG concentration should have been included in the comparison but there were no samples left.

After the last experiments to determine what cell line to use, it was determined that an expression that compares other expression variables should be run. This optimization used NiCo at 16C, since this had the best expression. Two medias, LB and TB were used. Two time points were taken, one at 16 hours after induction and another at 24 hours after induction. Three different induction densities were compared, 0.3, 0.6, and 0.9. The IPTG concentrations were 0.03, 0.1, and 0.3mM. For the lysis, 5mM BME should have been added, but it was not added to the 16-hour time point.

2.5.2 Large Scale Expression

The first large scale expression was run and then purified by the fast protein liquid chromatography. 100ml (with 100ul amp) was inoculated with 1ml of overnight outgrowth and four hours later was induced at 0.765 OD600. It was left overnight at 16C and shaken at 225 rpm. The following day the cultures were transferred to 50 ml falcon tubes, spun down, and the supernatant was taken off. The amount of BugBuster to be added to the lysis was determined. Since there was 0.3g of wet pellet, 1.5 ml of BugBuster was added (5ml BugBuster per 1g wet cell paste) with protease inhibitor (1tablet/ 10ml). Then the solution was incubated on the nutator, divided up among 1.5 ml tubes, spun at 4C, and then the total cell lysate and cleared cell lysate fractions were collected. The fractions were put in –20C, however they should have been flash frozen with liquid nitrogen and stored at –80C.

The second large scale expression was conducted to produce aliquots for the solubility rescue strategy of a lysis conditions screening. On day 1 of the experiment, the TF-PA fusion in NiCo cell strain glycerol stock was stabbed and then swirled into 3 ml LB with 3 ul amp. This culture was shaken overnight at 37C and 225 rpm. On day 2, 1ml of the overnight culture was

added to 100 ml of fresh LB/amp. After 2 hours, at 0.58 OD600, 9.8 ul of 1 M IPTG to have a 0.1 mM IPTG concentration. On day 3, 20 1 ml aliquots of cell media were made. The rest of the 48 ml of media was put in a falcon tube. The cultures were spun down, the media aspirated off, and the pellets flash frozen in liquid nitrogen and then stored at –80C. The large-scale expression of TF-PA was run through Fast Liquid Chromatography (FPLC). Our protein constructs are His-tagged, so a HisTrap column was used, followed by size exclusion on a Sephacryl S200 column. The protein peak revealed that it was the correct molecular weight to be TF-PA for the HisTrap column, but there was little success with size exclusion.

2.6 Rescue Strategies

2.6.1 Co-Expression with Polymerase Basic Protein

In hopes to increase solubility, PB1 and PA (Appendix C) were co-expressed. This was done first by designing and creating a gene that is the portion of PB1 that binds into the pocket of PA. This gene was called 3HB-strep2-PB1(1-27). PB1 was inserted with molecular biology techniques into two different vectors, the first just a normal empty vector called pACYC- LIC+ (Appendix A) and the second a vector that contained a folding chaperone (GroEL/Es) and TF, called pACYC GroEL/ES-TF (Appendix A). The GroEL/Es-TF vector inserts were both replaced with PB1. In other words, PB1 either replaced TF in the vector or GroEL/Es. This was done through double restriction enzyme digests and ligations. Then, the PB1 vectors were co-transformed with selected PA fusion vectors. After transformation the co-expression with two antibiotics was run.

2.6.1.1 Restriction Enzyme Double Digests

The PB1 gene (synthesized by Genscript) was cut with NdeI/BSA1, NdeI/XhoI, NiCoI/hindIII so that it could be ligated with vectors that were cut with corresponding restriction

enzymes. pACYC-LIC+ (AddGene) was cut with NdeI/Bsa1. pACYC-GroEL/ES-TF was cut with NiCo1/HindIII and NdeI/XhoI.

The following reactants were pipetted and then centrifuged in an epitube:

vector	LIC+	PB1	GroEL/ES-TF	PB1	GroEL/ES-TF	PB1
Nuclease-free water	33 uL	40	28 uL	40	28	40
10X CutSmart Buffer	5µl	5	5µl	5	5	5
Enzyme 1	NdeI*	NdeI	NcoI	NcoI	NdeI	NdeI
Enzyme 2	BsaI	BsaI	HindIII	HindIII	XhoI	XhoI
[Vector]	10	3	15	3	15	3

*all restriction enzymes will be 1ul because all enzymes used had concentrations of 20000 units/ml (One unit is defined as the amount of enzyme required to digest 1 µg of pXba DNA in 1 hour at 37°C in a total reaction volume of 50 µl.)

After the components were combined, the tubes were spun at 15000rpm for 1 minute. The solutions were pipetted to mix, incubated at 37C for 30-60 minutes, and then heat inactivated at 80C for 20 minutes.

From <https://www.neb.com/protocols/0001/01/01/5-minute-transformation-protocol-c2987>

2.6.1.2 Gel purification and Extraction

The DNA solutions were purified by through gel purification and extraction. A 0.8% agarose was used. After electrophoresis, the DNA fragment was excised from the agarose gel with a clean, sharp scalpel, however it was difficult to visualize where exactly the DNA fragments were in the gel. So, it is uncertain if the DNA was actually captured. The gel slices were weighed and 3 volumes of Buffer QG was added to 1 volume gel (100 mg gel ~ 100 µl).

Vector	Tube (g)	tube+gel (g)	Gel (g)
LIC+ NdeI BsaI	0.9653	1.3177	.3524
Pb1 NdeI BsaI	0.9216	1.3286	.4070
Gro NcoI HindIII	0.9499	1.0794	.1295
PB1 NcoI HindIII	0.9640	1.3543	.3903

Gro NdeI XhoI	0.9500	1.0762	.1262
PB1 NdeI XhoI	0.9424	1.2455	.3031

Gel (mg)	Buffer QG
352.4	1057.2
407	1221
129.5	388.5
390.3	1170.9
126.2	378.6
303.1	909.3

The solutions were then incubated at 50°C for 10 min with vortexing every 2–3 min to dissolve the gel. 1 gel volume of isopropanol was added and mixed with the sample. The sample was applied to the QIAquick column to bind DNA and centrifuged for 1 min. The flow-through was discarded. 750 µl Buffer PE was added to QIAquick column and centrifuged for 1 min to wash. Again, the flow-through was discarded. The QIAquick column was centrifuged in the provided 2 ml collection tube for 1 min to remove residual wash buffer. The QIAquick column was placed into a clean 1.5 ml microcentrifuge tube. 50 µl Buffer EB (10 mM Tris·Cl, pH 8.5) was added to the center of the QIAquick membrane to elute DNA. Before centrifuging the column was left to stand for 1 minute.

2.6.1.3 Ligation

The following reactions were set up in a microcentrifuge tube on ice, in the following order: 1) water 2) T4 DNA Ligase Buffer 3) Insert DNA 4) Vector DNA 5) T4 DNA ligase

COMPONENT	**Lic+ 3:1**	**7:1**	**Gro NH 3:1**	**7:1**	**Gro NX 3:1**	**7:1**
T4 DNA Ligase Buffer (10X) *	2 µl	2 µl	2 µl	2 µl	2 µl	2 µl
Vector DNA	7 µl (40ng)	5.5 µl (27.5ng)	15.5 µl (41.85ng)	15.5 µl (41.85ng)	10 µl (69ng)	10 µl (69ng)
Insert DNA	7.6 µl (7.6ng)	12 µl (12ng)	1 µl (7.5ng)	1.96 µl (17.68 ng)	1.6 µl (13.93ng)	3.6 µl (32.5ng)
Nuclease-free water	2.4 µl	0 µl	1.4 µl	0 µl	5.4 µl	3.4 µl

T4 DNA Ligase	1 µl	1 µl	1 µl	1 µl	1 µl	1 µl

The reaction was gently mixed by pipetting up and down, incubated at room temperature for 60 minutes, heat inactivated at 65°C for 10 minutes, and put in –20C.

The sequencing of DLP37 and 38 demonstrated that ligation was not successful, so the process was repeated starting with digestion. Even after repeating, ligation of PB1 to the GroEL/ES- TF vector still failed, so only the PB1 gene in the empty vector was taken further.

2.6.1.4 Co-transformation of PA and PB1 Transformation of both DLP36 and PA-fusion into NiCo or T7 strain

The co-transformation consisted of the typical transformation protocol; however, both the PA fusion vectors and the PB1- pACYC- LIC+ vectors were added to the reaction. Double antibiotic selection was achieved by adding both ampicillin and chloramphenicol to the overnight cultures made from the transformation.

2.6.1.5 DLP36 and DLP17,18,19, 22 Co-Expression and analysis

Day 1, stabs from the glycerol stocks from both the PB1 plasmid and GFP-PA, NoFusion-PA, MBP-PA, and TF-PA were swirled in the same LB media inoculated with CPL, amp, and glucose and shaken over night at 37C and 275 rpm. Day 2, the expression was run for 16 hr. at 20C and 120 rpm. Day 3, the expression cultures were pelleted and the media was aspirated off. Then the cells were lysed with BugBuster with protease inhibitors and 50 ul DTT. Then they were incubated on a nutator for 10-20min at room temperature. The portion for TCL was collected. Then the solutions were spun for 20 min at 4C. After, the cleared lysate portion was collected from the supernatant.

2.6.2 Bacterial Lysis Additives

To create the lysis buffer, 2 ml of 100mM NaCl, 2 ml of 100mM Tris pH 8, 8ul of DTT, and 0.004g lysozyme were all mixed together. The following are dilutions of the lysis additives:

Additive	Concentration
Xylitol	1 M
Potassium citrate	0.1 M
Proline	0.5 M
Potassium phosphate	0.1 M
Glycerol	10 mM
D-mannitol	0.5 M
Trehalose	0.75 M
Arginine	0.375 M
Betaine	1 M

These intermediate dilution additives were combined 1:1 with lysis buffer. The DLP22 samples pellets from the second large scale expression were resuspended with the additive and lysis buffer mix. Then the solutions were incubated at room temperature for an hour on the nutator. The DNase solution was made, a 1 mg/ml stock was dilute 1:1000 in buffer. After incubation, 0.5ul of MgCl2 and 0.5ul of 1mg/ml Dnase was added. Then the solution was incubated for 20 minutes at 4C. To analyze the results of the lysis, an SDS-PAGE gel was run.

Chapter 3: Results and discussion

3.1 Successful Construction of DNA Vectors and Construction of PA-Fusion Vectors

A starting expression plasmid DLP002 (Daniels Lab Plasmid) derived from pET-21b (Appendix A) with adapted restriction sites and a non-expressing spacer insert (Appendix C), was amplified through transformation into NEB5a competent *E. coli*, then the bacterial cells were lysed, and the DNA was purified using a Qiagen miniprep kit. Following the transformation and purification by a miniprep kit, the yield was measured using a microplate spectrometer. DLP002 is 6091 bp and the size of the plasmid was confirmed by a Thermo Fischer E-gel electrophoresis kit, with a band appearing in the expected region of the gel. Because DLP002 is the plasmid that all other plasmids would

be built from, it was sent for confirmation sequencing by Genscript. The identity of the plasmid was confirmed. Following this, all inserts (Appendix C), including: green fluorescent protein (GFP), maltose binding protein (MBP), trigger factor (TF), GST, SUMO, Trx, GFPa, and no fusion which served as the control, were amplified from various source plasmids by polymerase chain reactions (PCR). After their size was confirmed through gel electrophoresis, all PCR reactions were then digested with restriction enzymes XhoI, NheI and DpnI. Instead of using electrophoresis to purify and recover DNA, as is customary, PCR reactions were purified by spin column (PCR cleanup kit), and electrophoresis was used just to assess the success of PCR. DLP002 was double digested with XhoI, NheI and CIP-treated. The PCR inserts and the DLP002 vector were then ligated with T4 DNA Ligase. The ligation reactions were transformed, colonies grown overnight, then purified by a miniprep kit. A Golden Gate reaction, which is the combination of a digestion and ligation in one step was performed on all the plasmids to insert PA or PAt. Plasmids were again transformed and purified by a miniprep kit. Glycerol stocks of the overnight inoculations for all ligation reactions were saved for a backup plasmid archive. Sequences were confirmed for the 16 vectors, 8 toolbox and 8 vectors that were carried onto protein expression (Appendix D).

3.2 Iterative Expression Tests to Increase Solubility

After determining the bacterial growth rate, the first expression with common conditions, 37C and 4-hour induction time with 1mM IPTG, was run. The results of the analysis showed that there is no soluble protein produced in either the growth test or the initial expression test; marking the first revelation of the insolubility problem or the first

indication that the protein is insoluble. Insolubility is demonstrated by large bands on the gel in the total lysate fraction, while the cleared has relatively no bands in the expected molecular kilodalton region. Various expressions were reiterated at least 18 times in hopes of finding conditions that would increase the solubility of the PA protein fusions. Different cell strains, IPTG concentrations, and temperatures were used. No conditions were found that entirely solved the solubility issue, though there were conditions that showed slightly more promising results.

3.2.1 Growth Tests and Initial Conditions

After being introduced into the expression bacterial strains, DLP17-21 and 28-32 were put through a test expression. The plate leaked and the media migrated around the plate, mixing different vector constructs and preventing conclusions about specific vectors success. To prevent the plates from leaking, various experiments were conducted to troubleshoot the problem. Varying amounts of LB broth were put in the plates in wells nonadjacent. The angle at which the plates were shook was varied. Finally, conditions were found with no leakage and proper aeration at 22.5° angle with a roller to seal porous adhesive to the plates.

Two growth tests were performed to determine the rate of growth and at what time the cell culture would reach a density of 0.6 OD at 600nm. Cultures were started at 5:00 pm with a stab of cell culture swirled in 3ml of LB media for growth overnight. In the morning, 30ul from the overnight growth were inoculated into 3ml. From these outgrowths, it was estimated that on average it took 1.5-2 hours to reach the appropriate

density (0.6OD) for the first vis-spec reading. The appropriate time for the density to double was determined to be from 20 to 40 minutes.

Since the initial growth test only gave the growth rate of one vector in NiCo and T7 in LB media, another growth test was conducted to find the normalization of the growth rate using two different vectors in LB and TB media. The results demonstrate that there is not an appreciable difference between the density of the two vectors, so the generalization that the vector does not have an effect on growth was concluded. The medias LB and TB for both vectors had very different density readings, demonstrating different growth rates. TB combined with NiCo had more than double the density than LB combined with NiCo. TB with T7 had a third more colonies than TB with NiCo.

DLP19 NiCo with LB: .825
DLP20 NiCo with LB: .823
DLP19 T7 with LB: 1.118
DLP20 T7 with LB: 1.106

DLP19 Nico with TB: 2.269
DLP20 Nico with TB: 2.1
DLP19 T7 with TB: 1.8
DLP20 T7 with TB: 1.88

3.2.2 IPTG Scanning and Temperature, Induction Density, and Media Variations

To increase the likelihood of soluble protein, various conditions for expression were tested. From literature sources, it was found that varying amounts of IPTG can be used for expression and that the temperature for expression is commonly 16°C with an overnight induction time of 16 hours. In addition to changing the temperature of the expression induction to 16C, we conducted panels of different IPTG concentrations ranging from 0.015mM to 1.5mM for the next expressions. Different concentrations of

IPTG and 16C temperature yielded no significant improvement in solubility, only slight differences. The initial density of cells at the time of induction was 0.6OD, later 0.4 and 0.8 OD were used for the induction density. This had no real impact on solubility. Since the media the cells grow in could have affected expression, we used terrific broth (TB) in replacement of LB broth. TB has added nutrients and is a richer broth; it yielded much higher densities of cells overall, but it did not increase solubility. In fact, it was believed that the quicker growth rate could actually hinder protein solubility. So, LB was the media that was typically used for expressions. Since the slight variations in media, IPTG concentration, induction density, and temperature did not increase solubility, another approach was needed.

3.2.3 Cell Strain Modifications

It was decided that the expression strains NiCo21 (DE3) Competent E. Coli. and T7 express competent E. coli (High Efficiency) Bacterial strains would be used. T7 express is a common strain that is used; NiCo was chosen because it has useful properties for protein purification. The results from this NiCo expression showed that the protein in fact was very insoluble.

It was decided that various bacterial strains could be utilized since expression through them can affect solubility. The three strains used were Arctic express, T7 shuffle, and tuner express.

Arctic express was chosen as it has a folding chaperone protein, which is derived from a cryophilic, so the expression must be run at 12C. The hope was that the chaperone would help the PA constructs become soluble by assisting in folding, if PA was

misfolding. The PA-TF construct was slightly soluble with this expression strain, as it was for other expression stains. Its highest solubility for this expression was at 1.0 IPTG concentration. The rest of the PA constructs were not soluble.

If the solubility issue is caused by disulfide bonds formation, the use of T7 shuffle could improve solubility by preventing the formation of disulfide bonds. Commonly, disulfide bonds form between cysteine residues of the protein chain and can cause misfolding driving insolubility. Using shuffle did not increase the solubility of the proteins, however it is too far of a logical leap to assume the solubility issue was not driven by disulfide bond formation. The next strategy attempted was to use tuner, an expression strain that responds to different amounts of IPTG concentrations. The MBP-PA construct may have had some soluble fraction at 0.045 IPTG concentration, but it could have also been background proteins.

3.2.4 Autoinduction Media Utilization

Another strategy to solve the solubility issue was to use in an autoinduction system growth media. The autoinduction system works by having a certain amount of glucose and lactose in the media. The media contains everything needed for the induction of the expression of the proteins, however the cell preferentially consumes glucose over lactose for energetic economy. Once the bacteria consume the excess glucose, lactose induces the expression of the T7 promoter gene begins. A homemade autoinduction media was created and a test expression was run; it appeared that the media did not induce the expression of proteins substantially as there were almost nonexistent bands in all the fractions.

Possibly the homemade autoinduction media did not have the exact components and appropriate component concentrations for successful autoinduction. This would explain why the bacteria did not induce. In order to determine if this was the case, a commercial autoinduction media, overnight express, was purchased. It was used to express the GFP-PA and NoFusion-PA constructs in T7 shuffle and T7 express cell strains at temperatures of 37°C and 16°C. Again, the induction of both was low since there were very faint bands in the total cell lysate lane. The NoFusion-PA construct, which serves as a control, in the T7 express cell line had questionable bands in the soluble fraction, so it could be somewhat soluble in these conditions, but it was most likely background. It had larger, though still very faint, bands in the 16C expression than the 37C expression.

3.3 Bacterial Lysis, Nickel Bead Purification, and SDS-PAGE Analysis

Figure 7 is of a gel of the total cell lysate followed by the depleted cell lysate of a TF-PA optimization experiment (see section *3.2.5 Direct Comparison Expression to Find More Optimal Conditions)*. As can be seen, the odd numbered lanes which contain the total cell lysate are only slightly darker than the depleted cell lysate bands in the even-numbered lanes. This shows that the nickel beads did not capture most of the protein, possibly because of protein aggregation. Since there was not enough purified soluble protein from expressions that were added to the nickel magnetic beads to view expected bands, no conclusions could be drawn about the success of the pulldown. The proteins could be self-aggregating, so if put through a pulldown, the HisTag is not accessible to bind to the Ni beads.

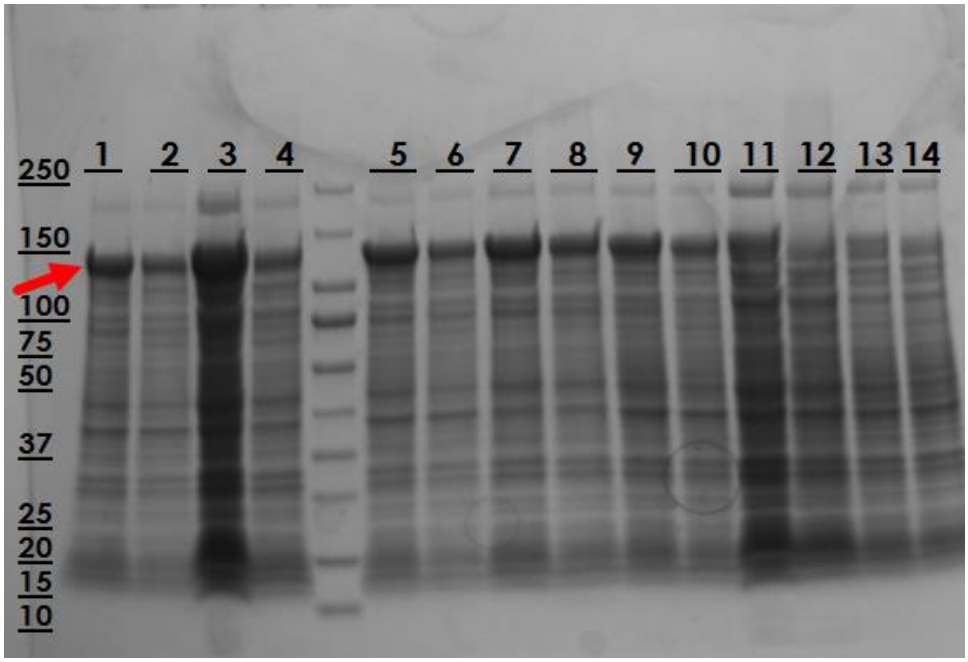

Figure 7 SDS-PAGE analysis of TF-PA Optimization with almost equal amounts of protein in the depleted lysate and total cell lysate fractions. There should be little to know protein in the depleted lysate fraction if the magnetic beads bound the protein, however it is evident that there is a large band, so the beads must not have bound the protein successfully.

To determine if it was the PA protein or the actual purification protocol that resulted in less than stellar results, a positive control pulldown was conducted using a PriB protein. The results revealed that there were faint bands in the wash and depleted lysate. The elution band and cleared lysate both had bright visibility, but the elution band is only very slightly darker than the cleared lysate, it should be much darker as it is four times as concentrated. The faint bands of the wash and depleted and the only slightly darker band in the elution indicate that some protein is lost to the pulldown procedure. For the most part, the pulldown is effective if enough soluble protein is added.

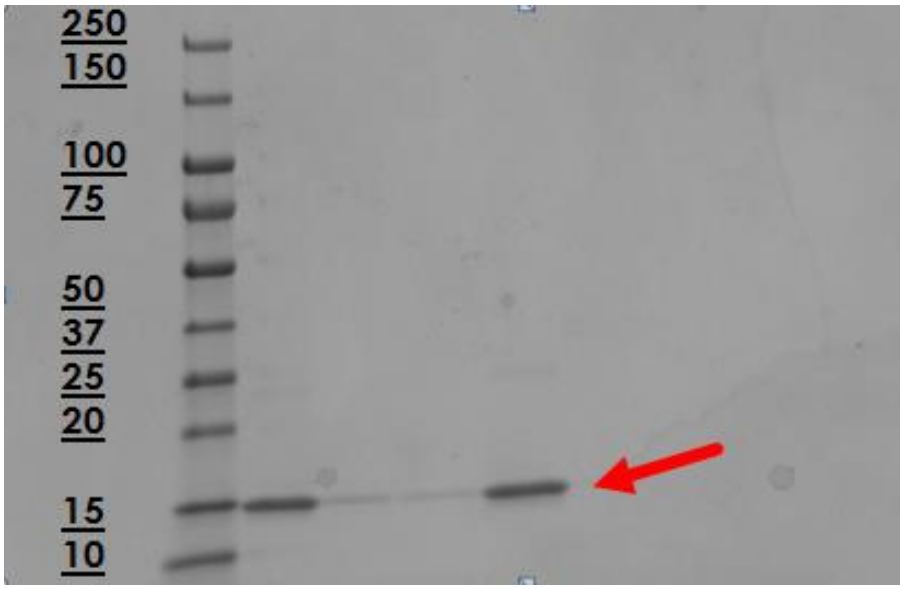

Figure 8 The elution band (red arrow) has a considerable band that is much more visible than the depleted and cleared lysate bands. The darker elution band indicates that the purification protocol is successful if enough soluble, non-aggregated protein is used.

Though there is no specific test conducted to support this, there is no reason to believe the SDS PAGE analysis protocol is flawed.

3.4 TF-PA Optimization and Large-Scale Expression Test

3.4.1 Direct Comparison Expression to Find More Optimal Conditions

After every PAGE analysis of expressions, images of the gels are obtained, however the gel images had varying exposure for each iteration, making the comparison between different expressions somewhat inaccurate. In addition, many different variables of purification and SDS-PAGE analysis affect the comparison between expressions.

In order to normalize the conditions for comparison between expressions, another experiment was run. The PA-TF construct was the only protein that had enough solubility to be taken to expression on a large scale. The leftover samples from previous expressions that were estimated to have the highest yields of soluble protein for PA-TF

were purified through nickel magnetic bead protocol and then analyzed with SDS-PAGE. Tuner, artic express, and shuffle were strains that were chosen for the comparison. The NiCo expression did not have any leftover samples to run. The results from this analysis showed that shuffle had the best expression. However, upon further investigation it was found that Nico had solubility comparable to shuffle. Since NiCo is more traditional, its inherent characteristics aid with purification, and it is less expensive, it was used for the optimization instead of T7Shuffle.

The optimization experiment was an expression of PA-TF with two different times, two different uninduced controls, three different induction densities, three different IPTG concentrations, and in two different medias to find the conditions that resulted in the highest solubility of the protein fusion. The results showed no bands in the elution fraction and large bands in the depleted lysate. There must not have been enough soluble protein for the pulldown to be successful, even though there were large bands in the cleared lysate. NiCo at 16C in LB media with an IPTG concentration of 0.1mM had the brightest cleared lysate band.

Lane	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ind. Density	.3		MW		.6			.9			.3		.6		
Media	LB														
Fraction	CL										T	D	T	D	
[IPTG]	.03	.1		.3	.03	.1	.3	.03	.1	.3	.3	.3	.03	.03	

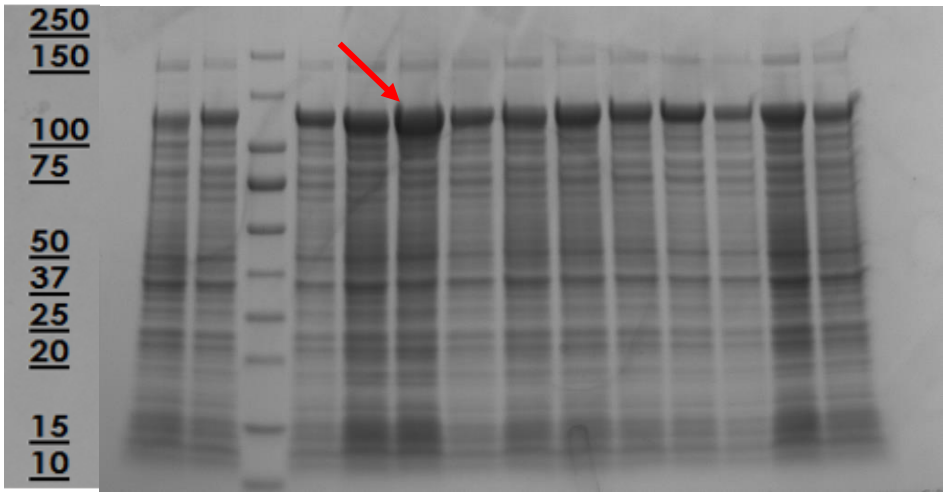

Figure 9 The conditions that had the highest solubility were 0.1 mM IPTG and 0.6OD induction density and the table above the gel image shows the expression conditions.

3.4.2 Large Scale Expression Tests

The PA-TF construct was expressed on a large scale and was purified through FPLC. The FPLC did show a peak in the current molecular weight. This confirmed and purified protein was also run through the nickel purification to test the competence of the purification. Interestingly, a cleared lysate fraction band of this purified protein was not visible on the SDS-PAGE, where it was expected. There appeared to be no TF-PA in the cleared lysate and depleted lysate fractions, and there are no visible proteins in the elution. There must not have been enough protein for the nickel purification to be successful. The FPLC purified proteins may have precipitated out with repeated freeze- thaw cycles.

An experiment was designed to find the missing protein. If the reason there appeared to be no protein is that it became insoluble during a freeze-thaw cycle and then a spin, then the protein may be found in the next experiment. It was believed that possibly the protein was spun down by accident. Samples of purified protein were mixed, left undisturbed and then spun down providing a supernatant fraction. All of these were used for the nickel

purification and then analyzed with SDS-PAGE analysis. Three different samples of purified samples had bands in the mixed and non-distributed samples, but not in the supernatant. There was no protein in the supernatant, so the evidence points to selected sample pull down the protein was actually spun out. However, the one protein sample that went through the most freeze-thaw cycles had the lightest band. This leads us to believe that freeze thaw cycles caused the protein to precipitate out. This was repeated with just one purified protein the pulldown showed no protein. This provides more conclusive evidence that free-thaw cycles cause the protein to precipitate out.

3.5 Solubility Enhancing Strategies

After numerous failed attempts to modify expression conditions, it was decided that a new strategy should be implemented.

3.5.1 Polymerase Basic Protein 1 Co-Expression

This new strategy is to co-express PB1 with PA. PB1 is naturally found with PA, and we believed that by including PB1 it would help PA to not aggregate upon itself in misfolding. The PB1 rescue strategy consisted of ordering two new vectors, the pACYC-GroEL/ES-TF vector with trigger factor protein and GroEL/ES protein and the PCYC-Lic+ vector, which was just an empty vector. The pACYC GroEL/Es-TF vector and PB1 were digested with NdeI and XhoI restriction enzymes to replace trigger factor with PB1 through ligation. In the same way, the restriction enzymes used to replace the GroEL/ES sequence with PB1 were Nico1 and HindIII. PB1 was also inserted into the pACYC-Lic+ vector with Nde1 and Bsa1 restriction enzymes. The creation of the pACYC-GroEL/ES-

TF with PB1 replacement vectors failed, however PB1 insertion into pACYC-Lic+ vector was confirmed with sequencing. The pACYC-Lic+/PB1 vector was carried through the rest of the experiment, without the two pACYC GroEL/ES-TF/PB1 vectors. It was transformed with multiple of the PA vectors including GFP-PA, NoFusion-PA, MBP-PA, TF-PA and GST-PA. The expression with Nico cell strain at 20° overnight at 150 RPM shake speed did not result in increased solubility. However, only one experiment was run. Possibly more experiments with more traditional conditions would increase solubility.

3.5.2 Lysis Additives Experiment

This experiment was only run once so conclusive decisions about its success rate cannot be made. More experiments will be run to determine how solubility can be increased with the lysis modification approach.

3.6 Conclusions

A series of 24 plasmids were successfully constructed. Eight of these are "toolbox" plasmids containing a common fusion protein ready to receive a protein of interest as an N-terminal fusion, and can be used in future projects. Sixteen plasmids are expression vectors containing PA or PAt proteins. Overall, our expressions and lysis protocols resulted in primarily insoluble PA. Crystallography experiments could not be performed as no construct resulted in protein that was soluble enough to carry to this next stage of the project. TF-PA had the highest amount of soluble protein since it had the largest band in the cleared cell lysate fraction on an SDS-PAGE, though it did not purify well. Expression conditions that were found to be best for TF-PA were NiCo cell strain, 16C, 0.1mM IPTG, 0.6OD induction density, and LB media. The co-expression of PB1 with PA did not considerably increase solubility in a single experiment.

More work could be done on this front. The lysis additive experiment should be repeated and it should be attempted with other protein constructs since only TF-PA was used in the lysis.

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Appendix A

Starting Plasmids

DLP1- from C. Garvie, Broad Institute, parent chain: pET21b

TGGCGAATGGGACGCGCCCTGTAGCGGCGCATTAAGCGCGGCGGGTGTGGTGGTTACGCGCAGCGTGACCGCTACACTTGCCAGCGCCCTAGCGCCCGCTCCTTT
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DLP2- starting plasmid (DLP1) with spacer inserted

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a

PB1-pUc51 plasmid sequence:

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Appendix B

Primer Sequences and Annealing Temperatures

BBSpacer-F:
ATCTGAGGATCCGAGACCATGGAAGAGAAACACATGCCTC
Tm:55/67
Tm: 61.7/73.6

BBSpacer-R:
AACTACGCTAGCTTCACGCAGATAGTGCAGATG
Tm:55/64
Tm: 61.3/70.5

MBP-F:
GCTAGGGCTAGCGGTCTCGGTAGCAAAATCGAAGAAGGCAAACTGG
Tm: 54/69.6

MBP-R:
TCTAGGCTCGAGTTAGGTCTGGGCATCTTTCAGGG
Tm: 57/66

GFPa-F:
ATCAATGCTAGCGGTCTCGGTAGCGAAGAGCGTAAAGCAGCGAAAGGTGAAGAACT
GTTTAC
Tm: 47.7/70

GFPa-R:
CGTTATCTCGAGTTATTTGTACAGTTCATCCATAC
Tm: 48/58

GST-F:
TACTAAGCTAGCGGTCTCGGTAGCGCAGGTACAGCAAGTCCGATCCTGGGCTATTG
Tm: 59/71

GST-R:
ACTATTCTCGAGTTATTTCGGCGGGTGATCGCCACC
Tm: 64/67

GFP-F:
ATCATTGCTAGCGGTCTCGGTAGCGCAAGTGATGGTGGCACC
Tm: 60/76

GFP-R:
CATGATTCTCGAGTTATTTGTACAGTTCATCCATACC
Tm: 52/62

NoFusion-F:
ATACTTGCTAGCGGTCTCGGTAGCTAACTCGAGTAGGA
Tm: 52/66

NoFusion-R:
TCCTACTCGAGTTAGCTACCGAGACCGCTAGCAAGTAT
Tm: 52/

TF-F:
TACTAAGCTAGCGGTCTCGGTAGCCAGGTTAGCGTTGAAACCACCCAG
Tm: 63/75

TF-R:
TCTAGCCTCGAGTTAGGCTTGCTGATTCATCAGTTCGTTAAAGGTGG
Tm: 65/71
Anneal: 58/66

Trx-F:
TACTAAGCTAGCGGTCTCGGTAGCAGCGACAAAATCATCCACCTGAC
Tm: 60/73

Trx-R (reduced 3 nt from original):
TCTAGCCTCGAGTTACCGCCAGGTTCGCGTC
Tm: 64/73
Anneal: 55/68

SUMO-F:
TACTAAGCTAGCGGTCTCGGTAGCAGCGATAGCGAAGTTAATCAAGAAGC
Tm: 60/72

SUMO-R (reduced 3 nt from original design):
TCTAGCCTCGAGTTAACCACCAATCTGCTCACGATGTGC
Tm: 65/71
Anneal: 55/66

Appendix C
DNA Inserts and Gene Sequences

Synthetic PA gene:
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PA-t gene:
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GACC

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GFP
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NoFusionAnnealed
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Appendix D

PA-Fusion Protein Sequence Plasmids

	PA	PA-t
GFP	17	28
No fus	18	29
MBP	19	30
GFPa	20	31
GST	21	32
TF	22	33
Trx	23	34
Sumo	24	35

Table of Fusions with associated DLP number

DLP17
TGGCGAATGGGACGCGCCCTGTAGCGGCGCATTAAGCGCGGCGGGTGTGGTGGTTACGCGCAGCGTGACCGCTACACTTGCCAGCGCCCTAGCGCCCGCTCCTTTCGCTTTCTTCCCTTCCTTTCTC
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AT

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