RESSALVA

Atendendo solicitação do(a) autor(a), o texto completo desta tese será disponibilizado somente a partir de 15/07/2018.

UNIVERSIDADE ESTADUAL PAULISTA "JÚLIO DE MESQUITA FILHO"
FACULDADE DE CIÊNCIAS AGRONÔMICAS
CAMPUS DE BOTUCATU

TOWARDS UNDERSTANDING THE INFLUENCE OF SEED MATURATION ON PHYSIOLOGICAL SEED QUALITY IN LEGUMES

RUBIANA FALOPA ROSSI

Thesis submitted to the College of Agricultural Sciences, UNESP- Botucatu to obtain the title of Doctor of Agronomy (Agriculture).

BOTUCATU - SP
July – 2016

UNIVERSIDADE ESTADUAL PAULISTA "JÚLIO DE MESQUITA FILHO"
FACULDADE DE CIÊNCIAS AGRONÔMICAS
CAMPUS DE BOTUCATU

TOWARDS UNDERSTANDING THE INFLUENCE OF SEED MATURATION ON PHYSIOLOGICAL SEED QUALITY IN LEGUMES

RUBIANA FALOPA ROSSI

Supervisor: Prof. Dr. Edvaldo Aparecido Amaral da Silva
Co- Supervisor: Prof. Dr. Olivier Henri Leon Leprince

Thesis submitted to the College of Agricultural Sciences, UNESP- Botucatu to obtain the title of Doctor of Agronomy (Agriculture).

BOTUCATU - SP
July – 2016

FICHA CATALOGRÁFICA ELABORADA PELA SEÇÃO TÉCNICA DE AQUISIÇÃO E TRATAMENTO DA INFORMAÇÃO – DIRETORIA TÉCNICA DE BIBLIOTECA E DOCUMENTAÇÃO - UNESP – FCA – LAGEADO – BOTUCATU (SP)

Rossi, Rubiana Falopa, 1986-
R833t Towards understanding the influence of seed maturation on physiological seed quality in legumes / Rubiana Falopa Rossi. – Botucatu : [s.n.], 2016
xiv, 157 f. : ils. color., tabs.

Tese (Doutorado) - Universidade Estadual Paulista, Faculdade de Ciências Agronômicas, Botucatu, 2016
Orientador: Edvaldo Aparecido Amaral da Silva
Coorientador: Olivier Henri Leon Leprince
Inclui bibliografia

1. Soja - Sementes - Qualidade. 2. Soja - Sementes – Desenvolvimento. 3. Germinação. 4. Longevidade. I. Silva, Edvaldo Aparecido Amaral. II. Leprince, Olivier Henri Leon. III. Universidade Estadual Paulista "Júlio de Mesquita Filho" (Câmpus de Botucatu). Faculdade de Ciências Agronômicas. IV. Título.

UNIVERSIDADE ESTADUAL PAULISTA

Câmpus de Botucatu

CERTIFICADO DE APROVAÇÃO

TÍTULO DA TESE: TOWARDS UNDERSTANDING THE INFLUENCE OF SEED MATURATION ON PHYSIOLOGICAL SEED QUALITY IN LEGUMES

AUTORA: RUBIANA FALOPA ROSSI
ORIENTADOR: EDVALDO APARECIDO AMARAL DA SILVA

Aprovada como parte das exigências para obtenção do Título de Doutora em AGRONOMIA (AGRICULTURA), pela Comissão Examinadora:

Prof. Dr. EDVALDO APARECIDO AMARAL DA SILVA
Dep de Produção e Melhoramento Vegetal / Faculdade de Ciencias Agronomicas de Botucatu

Prof. Dr. JOSÉ MÁRCIO ROCHA FARIA
Dep de Ciências Florestais / Universidade Federal de Lavras

Prof. Dr. OLIVIER HENRI LEON LEPRINCE
Agrocampus Ouest - França

Dra. JULIA BUITINK
INRA - França

Dra. NATHALIE NESI
UMR - França

Nathalie NESI

Botucatu, 15 de julho de 2016

I dedicate my thesis to my dear parents

João Rossi and Silvia Helena Falopa.

You are everything in my life.

ACKNOWLEDGEMENTS

One day I was told that the acknowledgements section of the thesis or dissertation is reserved to thank those who contributed directly to the accomplishement of the work in question. This looks easy, but for me this it is a little complicated. How restricting in few words something as broad as my gratitude? Throughout my walk there were so many people who contributed to my professional and personal growth. I don't even know where to begin.

Perhaps a good start is to begin to thanks my supervisors. In chronological order: Prof. Dr. Stela Maris Kulczynski was my first supervisor. Thank you to have shared with me your passion: the research. And thank you for teaching me to "look with the eyes of those who want to see". I will never forget that phrase.

Then, I started my activities in Botucatu and I had the honor of being received by Prof. Dr.Claudio Cavariani who guided me during my master studies. It was from him that I had my first official professional conversation and since then I carry with me your advices. Thank you, not only for your guidance, but for sharing with me your sincere friendship.

After that, Prof. Dr. Edvaldo A. A. da Silva became my PhD supervisor. Thank you for having supervised me, for believing in my work and for giving me the opportunity to do part of my doctorate in Angers-France. Thank you very much for contributing to my professional and personal growth.

To my supervisor in Angers Prof. Dr. Olivier Leprince. I am grateful for your supervision, guidance, suggestions and friendship; without your help I could not have finished my thesis successfully. Your commitment in seed science and encouragement made me to feel more confident to achieve my desire.

To Dr. Julia Buitink, I know you made many efforts to guide me. Thank you for your dedication and patience. It was a real pleasure to meet you in Angers and I have learned so much about seed science with you.

Participate in a sandwich doctorate program was great and wonderful challenge to me. To join the Conserto team was a privilege. Benoit Ly Vu, Joseph Ly Vu, David Lalanne, Julia Zinsmeister, Lucien Sahl, Shivan Yousif and friends group MitoStress e SESaN: Thank you very much! I really miss you all. Thank you for having received me and have not measured efforts to help me.

I want to thank a special person my dear Prof. João Nakagawa that was never officially my superviror, but at infinite time gave important suggestions to my work. It is beautiful to see your dedication to academic life. Even, more beautiful, is your lowness. You are admirable. Thank you!

In fact, the whole Department of Agriculture (FCA/Unesp), teachers, staff, technicians and colleagues, Vera Cereda, Amanda Bedetti, Eliane Gonçalves, Dorival Arruda, Thiago Gianeti and Iara Brito thanks for all assistance. A special thanks to Valeria Giandoni. A friend summarized what you mean to us in a simple phrase: "Valeria is the heart of the seed lab!!" And she's right. Thank you very much Val.

Célio Mariano, Casimiro Alves, Aparecido da Silva, Valdemir dos Santos, Milton Mateus, Antônio Camargo e Ciro de Oliveira, your help with the experiments in the field was essential.

The all friends of graduation course, especially partners and aggregates of the Seed Lab: Alexandre Carneiro, Pedro Bento, Thiago Alexandre, Vitor Maia, Leonel Pereira Neto, Girlanio Holanda, Júlio Maia, Andréia Akemi, Daiani Ajala, Letícia Moreno, Karina Ducatti, Victória Pires, Maria Rita Gilli, Bárbara Valario, Juliana Lima, Denise Basso, Bruna Luiza de Souza, Hellen Síglia Demétrio and Juliana Gimenez. To all of you thanks for your help and for sharing your knowledge and friendship above all. I always say that each new friendship, which we make throughout life, enriches us for what it reveals to us.

To Dr.Juliana Bravo, I want to extend my thanks on behalf of the entire seed laboratory. Ju, thank you for always help me. Thanks for your affection.

Lilian Silveira, Renake Teixeira and “Camilas” of my life: Camila Aquino and Camila Abrahão, thank you. It seems an exaggeration, but you were "sunshine on cloudy days". Each one in its particularity, and with special ways to speak, to advise and specially to hear. Anyway, I lack words to thank you all. I already miss you. I am a lucky person, because I have friends like you at my side.

I thank my longtime friend, Leandro Tropaldi, by sincere friendship and assistance from the graduation times to the present day. I hope our friendship lasts forever. Thank you!

Akeo Veerman, Gabriel Escobar, Raquel Lobo and David, thank you for making my days in Angers even more fun.

I would like to thank my godmother Isabel Falopa and my friends Mônica Aranha, Miriam Campos, Silvana Marques and Cristiane Cavalini who understood my absence, praying for my success and always expecting my return. Thank you.

I want share this moment with my eternal little Larissa Piccinin and my godson Arthur Teixeira. Thank you for understand my absence. I love both of you.

It is impossible to summarize what has been a doctorate in my life. I learned a lot, but I also discovered that I have much to learn; I found some answers, nevertheless, I found new questions. I overcame some fears and some obstacles. I met a wonderful person that has been important in my life. You encouraged me during my journey. To Danilo Almeida, my thanks for your affection, patience and constructive criticism. You were very important for the accomplishment of this project.

Lastly, I want to thank those people who are the basis, my safe haven: my parents, Silvia Helena Falopa and João Rossi. I left you for the last because without you nothing, absolutely nothing would be possible. Without your support, I would have retreated at the first obstacle. Nevertheless, you made a strong person. Thank you for investing in my dreams and be part of it. You are everything to me.

Now, a cycle has ended in my life. Cities, places and events, all a day passes.But, you, my friends, will continue with me, in my history and in my heart.

Thank you!
Merci beaucoup!

To the foundation institute,
São Paulo Research Foundation (FAPESP) for funding this
research by the consent of a scholarship
(FAPESP Process Nº: 2013/04598-8).

AGRADECIMENTOS

Um dia me disseram que a seção dos agradecimentos da tese ou da dissertação é o espaço reservado para agradecermos aqueles que contribuíram diretamente com a execução do trabalho em questão. Mas para mim isto está sendo um pouco complicado. Como restringir em breves palavras algo tão amplo quanto a minha gratidão? Ao longo da minha caminhada foram tantas pessoas que contribuíram para meu crescimento profissional e pessoal que eu nem sei por onde começar a agradecer.

Talvez um bom começo seja agradecendo meus orientadores. Em ordem cronológica, Prof. Dra. Stela Maris Kulczynski, minha primeira orientadora. A senhora, o meu muito obrigada. Obrigada por ter dividido comigo a sua grande paixão: a pesquisa e, por ter me ensinado a “olhar com olhos de quem quer ver”. Jamais esquecerei essa frase.

Em seguida, iniciei minhas atividades em Botucatu e tive a honra de ser recebida pelo Prof. Dr. Claudio Cavariani quem me orientou durante a execução do meu mestrado. Foi com ele que tive minha primeira conversa oficialmente profissional e, desde então carrego comigo suas colocações e conselhos. Professor meu muito obrigada, não só pela sua orientação, mas por partilhar comigo sua sincera amizade.

No doutorado fui orientada pelo Prof. Dr. Edvaldo Aparecido Amaral. Muito obrigada por ter me orientado, por ter acreditado em meu trabalho e por ter me dado a oportunidade de fazer parte do meu doutorado em Angers-Fr. Obrigada por ter contribuído para o meu crescimento profissional e pessoal.

Para meu supervisor em Angers Prof. Dr. Olivier Leprince. Sou grato pela sua supervisão, orientação, sugestões e amizade; sem a sua ajuda eu não poderia terminar a minha tese com sucesso. O seu compromisso com a ciência e o seu incentivo me fez sentir mais confiante para realizar meu desejo.

Para Dr. Julia Buitink, eu sei que você não mediu esforços para me auxiliar. Obrigado por sua dedicação e paciência. Foi um verdadeiro prazer conhecê-la em Angers e eu tenho aprendido muito sobre sementes com você.

Participar do programa de doutorado sanduíche foi um maravilhoso desafio e fazer parte da equipe ConSerto foi uma honra para mim. Benoit Ly Vu, Joseph Ly Vu, David Lalanne, Julia Zinsmeister, Lucien Sahl, Shivan Yousif e os amigos do grupo MitoStress e SESaN meu muito obrigada. Sinto muita saudade de vocês. Obrigada por terem me recebido e por não terem medido esforços para me auxiliar.

Quero agradecer aquele que, nunca foi oficialmente meu orientador, mas, por infinitas vezes desempenhou esse papel. Meu querido professor João Nakagawa, muito obrigada. Suas sugestões sempre foram importantes. Eu acho lindo de se ver sua dedicação à vida acadêmica. Ainda mais linda é a sua humildade. O senhor é admirável. Obrigada.

A todos do Departamento de Produção Vegetal – Agricultura, professores, funcionários, técnicos e colegas, meu muito obrigado. Vera Cereda, Amanda Bedetti, Eliane Gonçalves, Dorival Arruda, Thiago Gianeti e Iara Brito obrigada por toda ajuda. Um agradecimento especial a Valéria Giandoni. Uma amiga resumiu o que você significa para nós em uma simples frase: “a Valéria é o coração do laboratório de sementes!”, e ela tem razão. Muito Obrigada Val.

Célio Mariano, Casimiro Alves, Aparecido da Silva, Valdemir dos Santos, Milton Mateus, Antônio Camargo e Ciro de Oliveira, pela essencial contribuição nas atividades do experimento.

A todos os amigos do curso de pós-graduação, em especial os companheiros e agregados do Laboratório de Análise de Sementes: Alexandre Carneiro, Pedro Bento, Thiago Alexandre, Vitor Maia, Leonel Pereira Neto, Girlanio Holanda, Júlio Maia, Andréia Akemi, Daiani Ajala, Letícia Moreno, Karina Ducatti, Victória Pires, Maria Rita Gilli, Bárbara Valario, Juliana Lima, Denise Basso, Bruna Luiza de Souza, Hellen Síglia Demétrio e Juliana Gimenez. A todos vocês obrigada pela ajuda nos trabalhos, pelos conhecimentos divididos e pela amizade acima de tudo. Eu gosto de afirmar que cada novo amigo que ganhamos no decorrer da vida nos enriquece, nos aperfeiçoa, não tanto pelo que nos dá, mas pelo que nos revela de nós mesmos.

A Juliana Bravo, eu quero estender meu agradecimento em nome de todo o laboratório de sementes. Ju, muito obrigada por estar sempre disposta a nos socorrer. Obrigada por seu carinho.

As minhas amigas Lilian Silveira, Renake Teixeira e as “Camilas” da minha vida: Camila Aquino e Camila Abrahão. Parece exagero, mas vocês foram “o sol em dias nublados”. Cada uma na sua particularidade, no seu jeito especial de falar, de aconselhar e principalmente de ouvir. Enfim, me faltam palavras para agradecê-las. Já sinto tanta saudade de vocês. Eu sou uma pessoa de sorte, porque eu tenho amigas como vocês ao meu lado.

Agradeço meu amigo de longa data, Leandro Tropaldi, pela sincera amizade e auxilio desde os momentos da graduação até os dias de hoje. Que nossa amizade prolongue por toda vida. Obrigada!

Akeo Veerman, Gabriel Escobar, Raquel Lobo e Dav Id obrigada por tornarem meus dias em Angers ainda mais divertidos.

Quero agradecer a minha madrinha Isabel Falopa e as minhas amigas Mônica Aranha, Miriam Campos, Silvana Marques e Cristiani Cavallini que compreenderam a minha ausência, rezando pelo meu sucesso e aguardando carinhosamente o meu retorno. Muito obrigada.

Eu quero dividir este momento com minha eterna pequena Larissa Piccinin e com meu afilhado Arthur Teixeira. Obrigada por entender minha ausência. Amo vocês.

É impossível resumir o que foi o doutorado na minha vida. Aprendi muito, mas também descobri que tenho muito mais para aprender. Encontrei algumas respostas, no entanto encontrei novas perguntas. Eu superei alguns medos e venci alguns obstáculos. No meio de tantos acontecimentos, eu conheci uma pessoa maravilhosa que tem sido importante na minha vida. Você me incentivou durante a execução do meu trabalho. À você, Danilo Almeida obrigada pelo seu carinho, sua paciência, suas correções e críticas construtivas. Você foi muito importante para a realização desse projeto.

E, por último, quero agradecer aqueles que são minha base, meu porto seguro: meus pais: Silvia Helena Falopa e João Rossi. Eu deixei para agradecer vocês por último, pois sem vocês nada, absolutamente nada disso seria possível. Sem o vosso apoio eu teria recuado no primeiro obstáculo. Mas, vocês me fortaleceram. Obrigada por investir nos meus sonhos e fazerem parte dele. Vocês são tudo para mim!

Agora um ciclo se encerra na minha vida, cidades, casas, acontecimentos, tudo um dia ficará para trás. Mas, vocês, meus amigos, continuarão comigo, na minha história e no meu coração.

Muito Obrigada!

Agradecemos à Fundação de Apoio à Pesquisa do Estado de São Paulo (FAPESP), pelo apoio financeiro e pela concessão da bolsa de doutorado (Processo FAPESP Nº: 2013/04598-8).

CONTENTS

TABLES

FIGURES

ABSTRACT

During seed maturation, germination, desiccation tolerance and longevity are acquired sequentially. Seed maturation is terminated by a desiccation phase that brings the embryo to a quiescent state. In the seed production chain, the stage of maturity at harvest is the first factor that influences seed longevity and crop establishment. After harvest, seeds are usually dried to water content compatible with long term storage and post-harvest treatments. However, there is a lack of understanding of how seed longevity is acquired during seed maturation and how premature drying impacts longevity and resumption of cellular activities during imbibition. This was addressed here by comparing transcriptome changes associated with maturation drying and imbibition of seeds of soybean and *Medicago truncatula*, harvested at an immature stage and mature dry stage. The immature stage corresponded to end of seed filling when longevity was not acquired while other vigor traits were acquired. Transcriptome characterization in soybean revealed that enforced drying was not similar to maturation drying *in planta,* which stimulated degradation of chlorophyll and synthesis of protective chaperones. Eighty-nine % of the differentially expressed genes during a 18h-imbibition period showed a similar pattern between immature and mature seeds, consistent with a comparable germination between stages. An analysis of the 147 transcripts that increased during imbibition of mature seeds but not in immature seeds suggested an activation of processes associated with shoot meristem development and DNA repair. These data were compared with imbibing immature and mature seeds of Medicago and revealed an overrepresentation of genes involved in phototropism, seed coat and innate immunity in mature seeds. This work should provide new tools to optimize harvest at maximum seed quality.

Keywords: seed quality, seed development, germination, longevity, RNAseq.

INFLUÊNCIA DA MATURAÇÃO DE SEMENTES NA QUALIDADE FISIOLÓGICA DE LEGUMINOSAS

Botucatu, 2016. 157p.

Tese (Doutorado em Agronomia/Agricultura) – Faculdade de Ciências Agronômicas, Universidade Estadual Paulista.

Autor: RUBIANA FALOPA ROSSI

Orientador: EDVALDO APARECIDO AMARAL DA SILVA

Co – Orientador: OLIVIER HENRI LEON LEPRINCE

RESUMO

Durante a maturação da semente, a germinação, a tolerância à dessecação e a longevidade são adquiridos sequencialmente. A maturação da semente termina com a fase de dessecação que traz o embrião a um estado de repouso. Na cadeia de produção de sementes, o estádio de maturação no momento da colheita é o primeiro fator que influencia a longevidade das sementes e estabelecimento da cultura. Após a colheita, as sementes são normalmente secas para um teor de água compatível com os tratamentos pós-colheita e armazenamento a longo prazo. No entanto, há uma falta de compreensão de como a longevidade das sementes é adquirida durante a maturação da semente e qual o impacto da secagem prematura na longevidade e na retomada das atividades celulares durante a embebição. Esta questão foi abordada aqui, comparando alterações transcriptoma associados com a secagem maturação e embebição de sementes de soja e *Medicago truncatula*, colhidos em um estádio imaturo e estádio seco maturo. A fase imatura correspondeu final de enchimento de grãos, quando a longevidade não foi adquirida enquanto outros traços de vigor foram adquiridos. A caracterização do transcriptoma de soja revelou que a secagem forçada não era semelhante à maturação de secagem na planta, o que estimulou a degradação da clorofila e síntese de chaperones de proteção. Oitenta e nove % dos genes diferencialmente expressos durante um período de 18 horas de embebição mostrou um padrão similar entre as sementes imaturos e maduros, consistente com uma germinação comparáveis entre os estágios. Analisando os 146 transcritos que aumentam durante a embebição de sementes maduras, mas não em sementes imaturas sugeriu uma activação dos processos associados ao desenvolvimento de meristema e reparação do DNA. Esses dados foram comparados com sementes imaturas e maturas de Medicago durante a imbebição e revelou uma sobre-representação de genes envolvidos no fototropismo, revestimento de sementes e imunidade inata em sementes maturas. Este trabalho deve fornecer novas ferramentas para otimizar a colheita de sementes no ponto máximo de qualidade.

Palavras-chave: qualidade de sementes, desenvolvimento de sementes, germinação, longevidade, RNAseq.

CONTRIBUTION À LA COMPRÉHENSION DE L'EFFET DE LA MATURATION DES GRAINES SUR LEUR QUALITÉ PHYSIOLOGIQUE CHEZ LES LÉGUMINEUSES.

Ecole Doctorale: Végétal, Environnement, Nutrition, Agroalimentaire, Mer (VENAM) Laboratoire d'accueil : UMR 1345 Institut de Recherche en Horticulture et Semences (IRHS).

Autor: Rubiana Falopa ROSSI

Directeur de thèse: Professeur Edvaldo Aparecido AMARAL DA SILVA

Co directeur de thèse : Professeur Olivier Henri Leon LEPRINCE

RÉSUMÉ

Pendant la maturation des graines, la germination, tolérance à la dessication et longévité sont acquises de manière séquentielle. La maturation s'achève par la dessication qui amène l'embryon à l'état de quiescence. Au cours de leur production, la maturité des graines à la récolte est le premier facteur qui influence la longévité et l'établissement de la culture lors du semis. Les graines récoltées sont ensuite séchées à une teneur en eau permettant leur conservation. On ne comprend pas comment la longévité est installée pendant la maturation et comment un séchage prématuré influence la longévité et la reprise des activités cellulaires pendant l'imbibition. L'objectif de la thèse était de répondre à ces questions en comparant les transcriptomes de graines immatures et matures de soja et *Medicago truncatula* pendant la dessication et l'imbibition. Les graines immatures furent récoltées après le remplissage avant la dessiccation, lorsque la longévité n'est pas encore acquise. Chez le soja, la comparaison des transcriptomes des graines immatures et matures montre que le séchage forcé n'est pas identique à la dessication *in planta* qui se caractérise par la synthèse de protéines chaperones. Plus de 89% des gènes différentiellement exprimés après 18 h d'imbibition présentent des profils d'expression identiques dans les graines immatures et matures, en accord avec la germination comparable de celles-ci. L'analyse des transcrits dont la teneur augmente uniquement pendant l'imbibition des graines mature suggère la mise en place de mécanismes de réparation. La comparaison de ces données avec Medicago montre que l'imbibition des graines matures se caractérise par une sur-représentation des gènes liés au phototropisme, à la testa et réponse immunitaire. Ce travail doit permettre le développement d'outil d'analyse de la maturité des graines lors de leur récolte.

1. INTRODUCTION

Soybean (*Glycine max*, 2n = 40 chromosomes) is a native legume from East of Asia and the first reports of its use are from 2838 B.C. in China (MORSE, 1950 according to BOZATO and BOZATO, 1987). In Brazil, the introduction of soybean took place in 1882 in the State of Bahia and the State of Sao Paulo (D'UTRA, 1882; DAFFERT, 1893, according to BOZATO and BOZATO, 1987). Currently, Brazil is the second largest soybean producer in the world, preceded only by the United States and according to the latest information released by CONAB, soybeans are cultivated in an estimated area of 33 million of hectares with an estimated production of 100 million tons and an average yield of 3037 kg ha^{-1} (CONAB, 2016). Soybean is a rich source of protein and oil and has been traditionally used for oil production, food and feed (QIU and CHANG, 2010).

With the continued increase in world demand for sources of plant oil and proteins, soybean production has spread rapidly to tropical regions. In Brazil, there is a continuous effort to increase its production, mainly by increasing its yield per area. Therefore, it is imperative to know the physical characteristics of the plant, its growth stages, the nutritional demand, requirements of water, thermal and photoperiodic for proper management practices to reach increasing in soybean yield. The proper establishment of a seed production field requires careful planning, including: the choice of the region, respecting the requirement of culture in relation the availability of water (ranging between 450 and 800 mm per cycle, being higher during germination to emergence and flowering to seed filling) and temperature (ranging between 20 °C and 30 °C); the choice of the area, considering the history, the crop rotation and the physical properties of the soil, such as fertility, drainage and topography; the choice of the cultivar analyzing the maturity group, always considering the latitude. Other care are also necessary, such as row widths, plant population (200–230 thousand plant per hectares, depending on cultivar), the weed control, pest insects control and diseases are also important in the management of culture. The sowing date is one of the factors that most influence the yield of soybeans. Seed germination and seedling emergence are favored by temperatures between 25 °C and 30 °C. Soil temperature below 10 °C results in delay in seed germination and subject to the action of soil-borne pathogens. For good seedling emergence, the soil should not exceed 85% of available water and not be less than 50%. In addition to the temperature and humidity requirements, it is necessary considered the photoperiod. Once the soybean is a term and photosensitive specie, it is subject to physiological and morphological changes when their demands are not met (SEDIYAMA et al., 1993; BERGAMIN et al., 1999; SANTOS 2008). The theoretical best time of soybean sowing in any area suitable to its cultivation, is between 30 and 45 days before the summer solstice, this time is considered sufficient for the plant meet its growing season and develop with height and size compatible to high productivity and mechanized harvesting. In general, the varieties adapted to Brazilian conditions are cycled between 90 and 150 days (EMBRAPA, 2011).

Allied to the good management practices, the use of high quality seeds are the first critical factors leading to crop yield. Seed quality consists of genetic purity, physical and physiological quality and seed health (POPINIGS, 1985). All this attributes are important to determine the quality of the seeds, but one in particular, has received more attention: the physiological quality. Represented by germination, vigor and longevity, the physiological quality determines the performance in the field, affecting establishment of the seedlings, plants development and crop yield (BEWLEY and BLACK, 1994).

The physiological quality traits are not acquired in the same time. The capacity to germinate is acquired prior to maximum dry weight. This is followed by the development of desiccation tolerance. Concomitantly, seed vigor is acquired, which is represented by greater speed of germination, uniform seedling establishment and tolerance of stressful conditions during germination. Good seedling establishment is essential for crop production to be sustainable and profitable and therefore, a critically important trait for farmers and growers. Finally, longevity increases in the last stages of development

(BEWLEY et al. 2013). Production of seeds with high physiological quality (or vigor) is a paramount to maintain soybean expansion. Ideally, the seed harvesting should occur when all the above characteristics reach their maximum levels. However, there is no consensus as to when this occurs during the maturation. On the one hand, agronomy and seed technology studies consider that physiological quality is maximum when the seed filling has ended (so-called mass maturity) and can decrease thereafter during the end of maturation drying or during seed processing (TEKRONY et al., 1979; OBENDORF et al., 1980; FRANÇA NETO et al., 2007; REN et al., 2009). This occurs because, sometimes, in agronomic crops, such as soybean, the emphasis on seed production is associated with dry weight accumulation and crop yield. On the other hand, for seed physiologist, physiological maturity refers to the developmental stage at which seeds achieve maximum viability and vigor, which is not necessarily correlated with seed filling. In many species, further maturation drying to 45% moisture is necessary to achieve maximum germination speed and absence of abnormal seedlings (ELLIS et al., 1987; ZANAKIS et al., 1994; CHATELAIN et al., 2012). Seed longevity, another key factor implicated in physiological quality increase continuously after seed filling until dispersal or harvest (ELLIS et al., 1987; ELLIS et al., 1993; PROBERT et al., 2007; CHATELAIN et al., 2012). For practical reasons, seeds are harvested during the maturation drying, otherwise they would be crushed during the harvest. Therefore, commercial harvest has to be delayed until the seed moisture decreases to levels that are compatible to harmless mechanical handling. During this period, the seeds that remain on the plant are highly prone to deterioration, particularly when humidity and/or temperature remain high, conditions that typically occur in tropical regions.

The quality of soybean seeds is partly affected by the genetic of the plant. The trend in breeding programs was initially to develop genotypes able for cultivation in tropical regions, at different latitudes. Continuously, has been sought to develop genotypes with desirable traits for resistance to diseases and pests. In the last years have been sought genotypes with increased in oil content, protein and lignin in seed and tolerance to water stress, aiming to be a way of stabilizing the productivity. The genetic variability among genotypes for quality seed is information that should be considered by breeders during the strain selection process. Since the genotypes can express themselves differently in relation to seed quality. An example is the difference of soybean genotypes for resistance to mechanical damage (CARBONELL and KRZYZANOWSKI, 1995) which has been related to the higher lignin content in soybean seed coat (CAPELETI et al., 2005). Susceptibility to mechanical damage is associated to its lignin content, while longevity and potential deterioration in the field have been related to the degree of permeability of the integument (SOUZA and MARCOS FILHO, 2001). An example is the variability among soybean cultivars varying in color of the integument. The integument black coloring soybeans exhibit slower imbibition, increased resistance to deterioration in field, greater thickness antifungal properties, and higher lignin content compared to light-colored seed coats (CHACHALIS and SMITH 2000; SANTOS et al., 2007; MERTZ et al., 2009; DELLAGOSTIN et al., 2011).

The genotype can influence the intensity of the deterioration process. However, the seed quality is more closely related to environmental factors than genetic factors. Several studies have demonstrated variability in soybean seed composition caused by field intemperism (KEIRSTEAD, 1952; KANE et al., 1997; WATANABE and NAGASAWA, 1990; OBENDORF et al., 1998; WILSON, 2004). Generally, the temperature variation is a considerable factor in the plant growth especially during seed development (DORNBOS JR., 1995; WILSON, 2004, REN et al., 2009). High temperatures linked to excessive rainfall during the maturation can result in seed deterioration, irreversibly affecting seeds germination and vigor (TEKRONY et al, 1980; COSTA et al, 1994).When soybean seeds develop under elevated temperature, it was observed an increase of total oil and oleic acid concentration in seeds, whereas linolenic acid decrease (REN et al., 2009; CARRERA et al., 2011) and there is a negative correlation between oil and protein in soybean seeds (WATANABE and NAGASAWA, 1990).

Difficulties on germination and reduced seed longevity may be associated with response to environmental stress during development. Variations are associated with low stachyose, sucrose, and other nonreducing soluble carbohydrates, and reduction of phosphorus stored in the form of phytic acid (myo-inositol-1-phosphate) (WILSON, 2004). At molecular level, it was observed changes associated with high temperature in FAD2 enzyme (HEPPARD et al., 1996) and heat shock proteins (HSPs) (NAGAO et al., 1995). Sucrose binding protein (SBP) plays a critical role in sucrose uptake in soybean seed (GRIMES et al., 1992). Through the proteomic analysis, Ren et al. (2009) were able to identify 20 proteins whose accumulations were changed due to high temperature. The authors stressed that high temperature during seed development results in changes in the vigor and longevity and changes in seed protein expression profiles.

The occurrence of green seeds at the end of the maturation process has been reported as another issue for Brazilian soybean growers. The green seed is a problem, because it reduces seed quality and oil quality (GOMES et al., 2003; ZORATTO et al., 2009, PÁDUA et al., 2009; TEIXEIRA et al., 2016). According to Teixeira et al. (2016) the chlorophyll retention is generally associated with pronounced increase in temperature, which leads to a rapid decrease in water content and impairment of the natural degreening. Therefore, the production of high quality seeds requires that the maturation and harvesting phases occur under mild temperatures (COSTA et al., 2003; FRANÇA-NETO et al., 2007). In Brazil there are studies analyzing the appropriate regions for the production of high quality soybean seeds. Agroclimatic zoning for the state of Parana (COSTA et al., 1994) and state of Minas Gerais (PÁDUA et al., 2014), was already performed, and the agroclimatic zoning for other regions has being researched.

While the late phase of seed development appears to be critical in order to harvest at maximum physiological quality and despite the lack of consensus as to when maximum seed vigor is acquired in soybean, we still lack basic knowledge of the molecular processes occurring during the late phase of maturation after seed filling when seed vigor is acquired. In soybean, transcriptome studies have generated a wealth of data describing seed development, mainly during embryogenesis and filling (HAJDUCH et al., 2005; HUDSON, 2010; JONES et al., 2010, LIBAULT, 2010; SEVERIN et al., 2010; ASAKURA et al., 2012; SHA et al., 2012, SHAMIMUZZAMAM and VODKIN, 2012; AGHAMIRZAIE et al., 2013). However all these transcriptome studies never included developmental stages after seed filling, while 20-40 days can pass between mass maturity and dry mature seeds depending on the environmental conditions during cultivation. In order to optimize harvesting processes to ensure high quality seeds, it is therefore essential to revisit the molecular events occurring during seed maturation in association with the acquisition of various characteristics associated with seed quality.

It is generally inferred that desiccation during seed maturation promotes the transition from a developmental mode to a germination-oriented program (BEWLEY and BLACK, 1994). In Arabidopsis, *De novo* transcription is not required for protein synthesis during early imbibition, suggesting that the initial phase of germination depends only on pre-existing “stored” mRNA, which have accumulated during seed development (RAJJOU et al., 2004). At maturity, dry seeds of Arabidopsis contain approximately 12000 transcripts which have been characterized (reviewed in WEITBRECHT et al., 2011). This implies that these transcripts must be synthesized during seed maturation. However, when this occurs has not been investigated. Also, not all stored transcripts are necessary for germination. The identity of the specific mRNAs required for germination and when they are synthesized during development is still not known. A recent study on arabidopsis showed that during the first 3h of imbibition seeds translate some mRNAs that were part of developmental program such as LEAs and storage proteins, indicating that a subset of stored mRNA in dry seeds are characteristic of the maturation program and did not disappear during maturation drying (GALLAND et al., 2014). It is not known whether an artificial drying treatment in immature seeds would induce a similar or entirely different profile of stored mRNA compared to maturation drying. Such information would be useful to provide putative molecular indicators to assess the maturity status of harvested soybean seeds and whether post-harvest drying during seed processing is sufficient to replace natural maturation drying.

Considering the fact that the soybean genome is not small, that during soybean seed imbibition many genes are expressed, and that are not only genes related to seed(ling) performance, making it difficult to separate gene expression related to germination and seed vigor from genes involved in other functions. The soybean genome size approximately 975Mb is captured in 20 chromosomes, with 56044 protein-coding loci and 88647 transcripts have been predicted (SCHMUTZ et al., 2010). According to Mudge et al. (2005), there are highly syntenic regions in the genomes of soybean and *Medicago truncatula*, that is, regions of gene content conserved between both species. These authors reported that the up to 75% of soybean genes are colinear with *M. truncatula*, therefore, an interesting way towards understand the mechanisms involved in germination and seed vigor would be compare soybean genoma with *M. truncatula*.

Thus, there is a lack of understanding of how seed longevity is acquired during seed maturation and how premature drying impacts longevity and resumption of cellular activities during imbibition. This was addressed here by comparing transcriptome changes associated with maturation drying and imbibition of seeds of soybean and *Medicago truncatula*, harvested at an immature fresh stage and mature dry stage.

After a brief literature review and presentation of material and methods, we will first present and discuss the results obtained on soybean then on *Medicago truncatula*, following the order of the different objectives described above

6. CONCLUSIONS

- ✓ The capacity to germinate was progressively acquired during early seed filling, between stages R5.5 and stage R6. ABA levels increased from stage R5.1 until R6, corresponding to a maximum. Thereafter, it declined progressively;

- ✓ Desiccation tolerance was acquired at stage R7.2. All parameters used to assess seed vigor indicated that maturity was obtained at stage R7.2. Nevertheless, longevity was still not fully acquired at this stage as it nearly doubled between stage R7.2 and R9;

- ✓ The transcriptome analysis shows that there are differences at the molecular level between seeds of stage R7.2 (immature) and R9 (mature). Soybean mature seeds revealed a significant over-representation of genes related to response to heat, protein-folding, response to ER stress and genes related to light;

- ✓ Degradation and synthesis of transcripts during imbibition are similar between immature and mature seeds;

- ✓ Radicle growth competence through transcriptional regulation is activated early during seed imbibition;

- ✓ Transcript associated with ABA-induced stress response, Chl degradation, phytate synthesis and chaperone function disappear rapidly during imbibition;

- ✓ Chloroplast-encoded transcripts that should disappear during maturation are rapidly degraded during imbibition of immature seeds;

- ✓ Imbibition-induced transcriptome profile associated with longevity highlights a putative DNA repair;

- ✓ The comparison of the transcriptome profile between soybean and *Medicago truncatula* during maturation showed a significant over-representation of genes such as PHY A, PHYB, NFXL-1, ABI1-like 1, and SCARECROW-like 14

.

7. REFERENCES

ABELES, F. B.; MORGAN, P. W.; SALTVEIT JR, M. E. **Ethylene in Plant Biology**, 2. ed. New York: Academic Press, 1992.

ACKERSON, R. C. Abscisic acid and precocious germination in soybeans. **Journal Experimental Botany**, Lancaster, v. 35, p. 414-421, 1984.

ADAMS, C.; FJERSTAD, M. C.; RINNE, R. W. Characteristics of soybean seed maturation: necessity for slow dehydration. **Crop Science Society of America**, Madison, v. 23, n. 2, p. 265-267, 1982.

AGHAMIRZAIE, D. et al. Changes in RNA splicing in developing soybean (*Glycine max*) embryos. **Biology**, Switzerland, v. 2, p. 1311-1337, 2013.

ALDRICH, S. R. Maturity measurements in corn and an indication that the grain development continues after premature cutting. **Journal of the American Society of Agronomy**, Madison, v. 35, n. 8, p. 667-680, 1943.

ALLEN, D. K.; OHLROGGE, J. B.; SHACHAR-HILL, Y. The role of light in soybean seed filling metabolism. **The Plant Journal**, Chichester, v. 58, n. 2, p. 220-234, 2009.

ALMOGUERA, C. et al. The HaDREB2 transcription factor enhances basal thermotolerance and longevity of seeds through functional interaction with HaHSFA9. **BMC Plant Biology,** London, v. 9, n. 75, 2009.

ANDERS, S.; HUBER, W. Differential expression analysis for sequence count data. **Genome Biology**, v. 11, R106, 2010.

ANDERSON, S. R. Development of pod and seed of birds foot trefoil as related to maturity and to seed yields. **Agronomy Journal**, v. 47, n. 10, p. 483-487, 1955.

ARC, E. et al. ABA crosstalk with ethylene and nitric oxide in seed dormancy and germination. **Frontiers in Plant Science.** v. 4, n. 63, 2013.

ASAKURA, T. et al. Global gene expression profiles in developing soybean seeds. **Plant Physiology Biochemistry**, v. 52, p.147-153, 2012.

BASBOUSS-SERHAL, I. et al. Germination potential of dormant and nondormant arabidopsis seeds is driven by distinct recruitment of messenger RNAs to polysomes. **Plant Physiology**, v. 163, n. 3, p. 1049-1065, 2015.

BAUD, S. et al. An integrated overview of seed development in *Arabidopsis thaliana* ecotype WS. **Plant Physiology and Biochemistry**. v. 40, n. 2, p.151-160, 2002.

BAUD, S. et al. WRINKLED1 specifies the regulatory action of LEAFY COTYLEDON2 towards fatty acid metabolism during seed maturation in Arabidopsis. **The Plant Journal**, v. 50, n. 5, p. 825-838, 2007.

BAZIN, J. et al. Role of relative humidity, temperature, and water status in dormancy alleviation of sunflower seeds during dry after-ripening. **Journal of Experimental Botany**, v. 62, n. 2, p. 627-640, 2011.

BELLALOUI, N. Soybean seed phenol, lignin, and isoflavones partitioning as affected by seed node position and genotype differences. **Food and Nutrition Sciences**, Stoneville, USA, n. 3, p. 447-454**,** 2012.

Bentsink, L. et al. Cloning of DOG1, a quantitative trait locus controlling seed dormancy in Arabidopsis. **Proceedings of the National Academy of Sciences of the United States of America**. v. 103, n. 45, p. 17042–17047, 2006.

BERGAMIN, M.; CANCIAN, M. A. E.; CASTRO, P. R. C. Ecofisiologia da soja. In: CASTRO, P. R. C.; KLUGE, R. A. (Org.). **Ecofisiologia de cultivos anuais**: trigo, milho, soja, arroz e mandioca. São Paulo: Nobel, p. 73-90. 1999.

BETHKE, P. C. et al. The arabidopsis aleurone layer responds to nitric oxide, gibberellin, and abscisic acid and is sufficient and necessary for seed dormancy. Plant Physiology. v. 143, n. 3, p. 1173-1188, 2007.

BETTEY, M.; FINCH-SAVAGE, W. E. Stress protein content of mature *Brassica* seeds and their germination performance**. Physiology & Biochemistry**, v. 8, n. 3, p. 347-355, 1998.

BEWLEY, J. D. et al. **Seeds: physiology of development, germination and dormancy.** 3rd ed. New York: Springer, 2013.

BEWLEY, J. D. Seed Germination and dormancy. **The Plant Cell**, v.9, p.1055-1066, 1997.

BEWLEY, J. D.; BLACK, M. **Physiology and biochemistry of seeds in relation to germination**. Development, germination and growth. v.1, Berlim: Springer Verlag, 1978, 306p.

BEWLEY, J. D.; BLACK, M. **Seeds**: physiology of development and germination. New York: Plenum Press, 1994. 445 p.

BLACKMAN, S.A. et al.. Maturation proteins associated with desiccation tolerance in soybean. **Plant Physiology**. v.96, p.868-874, 1991.

BLÖCHL, A.; PETERBAUER, T.; RICHTER, A. Inhibition of raffinose oligosaccharide breakdown delays germination of pea seeds. **Journal of Plant Physiology**, v. 164, p. 1093-1096, 2007.

BOGATEK, R.; GNIAZDOWSKA, A. Ethylene in seed development, dormancy and germination. **Annual Plant Reviews**, v. 44, p. 189-218, 2012.

BOTHA, F. C.; POTGIETER, G. P.; BOTHA, A. M. Respiratory metabolism and gene expression during seed germination. **Journal of Plant Growth Regulation**, v. 11, n. 3, p. 211-224, 1992.

BOUDET, J. et al. Comparative analysis of the heat stable proteome of radicles of *Medicago truncatula* seeds during germination identifies late embryogenesis abundant proteins associated with desiccation tolerance. **Plant Physiology,** v. 140, n. 4, p. 1418-1436, 2006.

BOZATO, R; BOZATO A. L.V. **A soja no Brasil**: história e estatística. Londrina, EMBRAPA-CNPSo, 1987. 61p. (Documentos, 21).

BRASIL. Ministério da Agricultura e Reforma Agrária. **Regras para análise de sementes**. Brasília, DF: SNAD/DNDV/CLAV, 2009. 398 p.

BRAY, E.A. Molecular responses to water deficit. Plant Physiology. v.103, p. 1035-1040, 1993.

BREVEDAN, R. E.; EGLI, D.B. Short periods of water stress during seed filling, leaf senescence and yield of soybean. **Crop Science**. v. 43, p. 2083-2088, 2003.

BUCKERIDGE, M. S.; SANTOS, H. P.; TINÉ, M. A. S. Mobilisation of storage cell wall polysaccharides in seeds. **Plant Physiology and Biochemistry.** v. 38, p.141-156, 2000.

BUITINK, J. et al. Transcriptome profiling uncovers metabolic and regulatory processes occurring during the transition from desiccation-sensitive to desiccation-tolerant stages in *Medicago truncatula* seeds. **The Plant Journal,** v. 47, n. 5, p. 735-750, 2006.

BUITINK, J.; LEPRINCE, O. Glass formation in plant anhydrobiotes: survival in the dry state. ***Cryobiology***, v. 48, n. 3, p. 215-228. 2004.

BUITINK, J.; LEPRINCE, O. Intracellular glasses and seed survival in the dry state. ***Comptes Rendus Biologies***, v. 331, n. 10, p. 788-795. 2008.

CÂMARA, G. M. S.; HEIFFIG, L. S. Fisiologia, ambiente e rendimento da cultura da soja. In: CÂMARA, G.M.S. **Soja**: tecnologia da produção II. Piracicaba: G.M.S. CÂMARA, 2000. p.81-120.

CAPELETI, I. et al. A new procedure for quantification of lignin in soybean (*Glycine max* (L.) Merrill) seed coat and their relationship with the resistance to mechanical damage, **Seed Science & Technoly**. v. 33, p. 511-515, 2005.

CARBONELL, S. A. M.; KRZYZANOWSKI, F. C. The pendulum test for screening soybean genotypes for seeds resistant to mechanical damage. **Seed Science and Technology**, v. 23, p. 331–339, 1995.

CARRANCO, R. et al. Repression by an auxin/indole acetic acid protein connects auxin signaling with heat shock factor-mediated seed longevity. **Proceedings of the National Academy of Sciences**, v. 10, n. 50, p. 21908-21913, 2010.

CARRERA, C. et al. Environmental variation and correlation of seed components in nontransgenic soybeans: protein, oil, unsaturated fatty acids, tocopherols, and isoflavones. **Crop Science Society of America**, v. 51, n. 2, p. 800-809, 2011.

CARVALHO, N. M.; NAKAGAWA, J. **Sementes**: ciência, tecnologia e produção. Jaboticabal: Funep, 2000. 588 p.

CENTRO DE PESQUISA METEOROLÓGICAS E CLIMÁTICAS APLICADAS A AGRICULTURA - CEPAGRI. **Clima dos municípios paulistas**: Botucatu. Disponível em: <http://www.cpa.unicamp.br/outras-informacoes/clima_muni_086.html.>.

CHACHALIS, D.; SMITH, M.L. Imbibition behavior of soybean (*Glycine max* (L.) Merril) accessions with different testa characteristics. **Seed Science andTechnology**, v. 28, n. 2, p. 321-331, 2000.

CHATELAIN, E. et al. Evidence for participation of the methionine sulfoxide reductase repair system in plant seed longevity. **PNAS,** v. 110, n. 9, p. 3633-3538, 2013.

CHATELAIN, E. et al. Temporal profiling of the heat stable proteome during late maturation of *Medicago truncatula* seeds identifies a restricted subset of late embryogenesis abundant proteins associated with longevity. **Plant Cell and Environment**, v. 35, p. 1440-1455, 2012.

CHAVES, A. L. S.; MELLO-FARIAS, P. C. D. Ethylene and fruit ripening: from illumination gas to the control of gene expression, more than a century of discoveries. **Genetics and Molecular Biology**, v. 29, p. 508-515, 2006.

CHEN, F.; NONOGAKI, H.; BRADFORD, K, J. A gibberellin-regulated xyloglucan endotransyglycosylase gene is expressend in the endosperm cap during tomato seed germination. **Journal of Experimental Botany**, Oxford, v. 53, n. 367, p. 215-223, 2002.

CHEN, H. et al. Transcriptome-wide mapping of pea seed ageing reveals a pivotal role for genes related to oxidative stress and programmed cell death. **Plos One,** v. 8, n. 10, p. e78471, 2013.

CLERKX, E. J. M. et al. Characterization of *green seed*, an Enhancer of *abi3-1* in Arabidopsis That Affects Seed Longevity. Plant Physiology, v. 132, n. 2, p. 1077–1084, 2003.

CONAB - COMPANHIA NACIONAL DE ABASTECIMENTO. **Acompanhamento de safra brasileira**: grãos, quinto levantamento. Brasília, DF, 2016. Disponível em: <http://www.conab.gov.br/OlalaCMS/uploads/arquivos/16_02_04_11_21_34_boletim_graos_fevereiro_2016_ok.pdf>.

CONTRERAS, S. et. al. Red to far-red ratio during seed development affects lettuce seed germinability and longevity. **HortScience**, v. 44, n. 1, p. 130-134. 2009.

COOK, D. R. *Medicago truncatula*— a model in the making!: Commentary. **Current Opinion in Plant Biology**, v. 2, n. 4, p. 301-304, 1999.

CORBINEAU, F. et al. Ethylene, a key factor in the regulation of seed dormancy. **Front. Plant Science**, v.5.p.1-5, 2014.

COSTA, N. P. et al. Qualidade fisiológica, física e sanitária de sementes de soja produzidas no Brasil. **Revista Brasileira de Sementes**, v. 25, n. 1, p. 128-132, 2003.

COSTA, N. P. et al. Zoneamento ecológico do Estado do Paraná para a produção de sementes de cultivares precoces de soja. **Revista Brasileira de Sementes**, v. 16, n. 1, p. 12-19, 1994.

CROWE, A. J. et al. The seed-specific transactivator, ABI3, induces oleosin gene expression. **Plant Science**, v. 151, n. 2, p. 171-181, 2000.

CUNHA, R.; CASALI, V. W. D. Efeito de substâncias reguladoras de crescimento sobre a germinação de sementes de alface. **Revista Brasileira de Fisiologia Vegetal**, Londrina, v. 9, n. 2, p. 121-132, 1989.

DEBEAUJON, I.; LÉON-KLOOSTERZIEL, K. M.; KOORNNEEF, M. Influence of the Testa on Seed Dormancy, Germination, and Longevity in Arabidopsis. **Plant Physiology**, v. 122, p. 403-413, 2000.

DELLAGOSTIN, M. et al. Dissimilaridade genética em população segregante de soja com variabilidade para caracteres morfológicos de semente. Revista Brasileira de Sementes**, v. 33, n. 4, p. 689 - 698, 2011.**

DELOUCHE, J. C.; BASKIN, C. C. Accelerated aging techniques for predicting the relative storability of seed lots. **Seed Science Technology**. v.1, p. 427-452, 1973.

DIERKING, E. C.; BILYEU, K. D. Raffinose and stachyose metabolism are not required for efficient soybean seed germination. **Journal of Plant Physiology,** v. 166, n. 12, p. 1329-1335, 2009.

DU, Z. et al. AgriGO: a GO analysis toolkit for the agricultural community. **Nucleic Acids Research**, v. 38, W64-70, 2010.

ELLIS, R. H.; HONG, T. D.; JACKSON, M. T. Seed production environment, time of harvest, and the potential longevity of seeds of three cultivars of rice. **Annals of Botany**, v. 72, p.583-590, 1993.

ELLIS, R. H.; HONG, T. D.; ROBERTS, E. H. The development of desiccation tolerance and maximum seed quality during seed maturation of six grain legumes. **Annals of Botany**, v. 59, p. 23-29, 1987.

ELLIS, R. H.; PIETRA FILHO, C. The development of seed quality in spring and winter cultivars of barley and wheat. **Seed Science Research**, v. 2, n. 1, p. 9-15, 1992.

EMBRAPA, EMPRESA BRASILEIRA DE PESQUISA AGROPECUÁRIA. Centro Nacional de Pesquisa de Solos. **Sistema brasileiro de classificação de solos.** Brasília, DF, 2006.

EMBRAPA, EMPRESA BRASILEIRA DE PESQUISA AGROPECUÁRIA. **Tecnologias de produção de soja:** região central do Brasil: 2011. Londrina, 2011. 255 p.

FARIAS, J.R.B. et al. Caracterização de risco de déficit hídrico nas regiões produtoras de soja no Brasil. **Revista Brasileira de Agrometeorologia**. Passo Fundo, v.9, n.3, p.415-421, 2001.

FARRANT, J. M. et al. An overview of mechanisms of desiccation tolerance in selected angiosperm resurrection plants. **Plant Stress**, v. 1, p. 72-84, 2007.

FEHR, W. R.; CAVINESS, C. E.; **Stages of soybean development**. Ames: Iowa State University of Science and Technology, 1977. 11 p.

FERREIRA, A. G.; BORGHETTI, F. **Germinação**: do básico ao aplicado. Porto Alegre: Artmed, 2004. 323 p.

FINCH-SAVAGE, W.E. et al. Seed dormancy release in Arabidopsis *Cvi* by dry after-ripening, low temperature, nitrate and light shows common quantitative patterns of gene expression directed by environmentally specific sensing. **Plant J**. v. 51, n. 1, p. 60–78, 2007.

FINKELSTEIN R. et al. Molecular aspects of seed dormancy. **Annual Review of Plant Biology**. n. 59, p. 387–415, 2008.

FINKELSTEIN, R. et al. Abscisic Acid Signaling in Seeds and Seedlings. **The Plant Cell**, v. 14, n. 1, S15-S45, Supplement 2002.

FRANÇA NETO, J. B. et al. **Tecnologia da produção de semente de soja de alta qualidade**. Londrina: Embrapa, 2007. 22 p. (Circular técnica, 40).

FRANÇA NETO, J. B. et al.**Tecnologia da produção de semente de soja de alta qualidade**. Embrapa- CNPSo, Londrina, 2007. 22 p. (Embrapa-CNPSo, circular técnica, 40).

FRANÇA NETO, J. B. Qualidade fisiológica da semente. In: FRANÇA NETO, J. B; HENNING, A. A. **Qualidade fisiológica e sanitária de semente de soja**. Londrina: EMBRAPA, 1984. p. 5-24. (Circular Técnica, 9).

FREY, A. et al. Maternal synthesis of abscisic acid controls seed development and yield in Nicotiana plumbaginifolia. **Planta**, n. 218, p. 958–964, 2004.

FRUGOLI, J.; HARRIS, J. *Medicago truncatula* on the Move! **The Plant Cell**, v. 13, n. 3, p. 458-463, 2001.

GALLAND, M. et al. Dynamic proteomics emphasizes the importance of selective mRNA translation and protein turnover during Arabidopsis seed germination. **Molecular & Cellular Proteomics**, v. 13, p. 252–268, 2014.

GALLAND, M.; RAJJOU, L. Regulation of mRNA translation controls seed germination and is critical for seedling vigor. **Frontiers in Plant Science**, v. 6, p. 1-3, 2015.

GALLARDO K. et al. Proteomics of *Medicago truncatula* seed development establishes the time frame of diverse metabolic processes related to reserve accumulation. **Plant Physiology,** v. 133, p. 664-682, 2003.

GALLARDO, K. et al. Proteomic analysis of Arabidopsis seed germination and priming. **Plant Physiology**, Rockville, v. 126, n. 2, p. 835-848, 2001.

GENTLEMAN, R. C. et al. Bioconductor: open software development for computational biology and bioinformatics. **Genome Biology**, v. 5, n. 10, R80, 2004.

GHASSEMI-GOLEZANI, K., LOTFI, R., NOROUZI, M. Seed quality of soybean cultivars affected by pod position and water stress at reproductive stages. **International Journal of Plant, Animal and Environmental Sciences**, v.3, p.119-125, 2012.

GHASSEMI-GOLEZANI, K.; MOUSABEYGI, T.; RAEY,Y.; AHARIZAD, S. Effects of water stress and pod position on the seed quality of chickpea (*Cicer arietinum* L.) cultivars. **Notulae Botanicar Horti Agrobotanici Cluj-Napoca**, v.38, n.1, 2010.

GOMES, M. S. O. et al. Effect of harvesting and drying conditions on chlorophyll levels of soybean (*Glycine max* L. Merr). **Journal of Agricultural and Food Chemistry**, v. 51, n. 6, p. 1634–9, 2003

GRELET, J. et al. Identification in Pea Seed Mitochondria of a Late-Embryogenesis Abundant Protein Able to Protect Enzymes from Drying. **Plant Biologists**, v. 137, p. 157-167, 2005.

GRIMES, H. D. et al. A 62-kD sucrose binding protein is expressed and localized in tissues actively engaged in sucrose transport. **Plant Cell,** v. 4, p. 1561–1574, 1992.

GUTIERREZ, L. et al. Combined networks regulating seed maturation. **Trends in Plant Science**, v. 12, p. 294-300. 2007.

HAJDUCH, M. et al. A systematic proteomic study of seed filling in soybean. Establishment of high-resolution two-dimensional reference maps, expression profiles, and an interactive proteome database. **Plant Physiology**, v. 137, n. 4, p. 1397-1419, 2005.

HAKE, S. et al. The role of KNOX genes in plant development. **Cell and Developmental Biology**, v. 20, p. 125- 51, 2004.

HAYES, R. G.; KLEIN**,** W**.** H. Spectral quality influence of light during development of *Arabidopsis thaliana* plants in regulating seed germination**. Plant &Cell Physiology,** v. 15, n. 4, p. 643-653**,** 1974.

HEGEMAN, C. E.; GRABAU, E. A. A novel phytase with sequence similarity to purple acid phosphatases is expressed in cotyledons of germinating soybean seedlings. **Plant Physiology**, v. 126, n. 4, p. 1598-1608, 2001.

HILHORST, H. W. M. A critical update on seed dormancy. I. Primary dormancy. **Seed Science Research**, Ardingly, Haywards Heath**,** v. 5, p. 61-73, 1995.

HOEKSLRA. E A. et al. Changes in soluble sugars in relation to desiccation tolerance in cauliflower seeds. **Seed Science Research**. v. 4, n. 2, p. 143-147, 1994.

HOEKSTRA, F. A. et al. Imbibitional leakage from anhydrobiotes revisited. **Plant, Cell and Environment**, v. 22, n. 9, p. 1121-1131, 1999.

HOEKSTRA, F.; GOLOVINA, E. A.; BUITINK, J. Mechanisms of plant desiccation tolerance. **Trends in Plant Science**, v. 6, n. 9, p. 431-438, 2001.

HOLDSWORTH, M.; BENTSINK, L.; SOPPE, W. Molecular networks regulating Arabidopsis seed maturation , after ripening , dormancy and germination. **New Phytologist**, v. 179, n. 1, p. 33– 54, 2008.

HOWELL, K. A. et al. Mapping metabolic and transcript temporal switches during germination in rice highlights specific transcription factors and the role of RNA instability in the germination process. **Plant Physiology,** v. 149, n. 2, p. 961-980, 2009.

HSING, Y. C. et al. Premature drying and germination in wild soybean seeds. **Taiwania**, v. 40, p. 73-81, 1995.

HUBER, S. C. et al. Canopy position has a profound effect on soybean 1 seed composition. **PeerJ.** v.13, n.4: 32452, 2016.

HUDSON, K. A**.** The circadian clock-controlled transcriptome of developing soybean seeds. **Plant Genome**, v. 3, p. 3-13; 2010.

HUNDERTMARK, M. et al. The reduction of seed-specific dehydrins reduces seed longevity in *Arabidopsis thaliana*. **Seed Science Research**, v. 21, n. 3, p. 165-173, 2011.

HUNT, L.; HOLDSWORTH, M. J.; GRAY, J. E. Nicotinamidase activity is important for germination. **The Plant Journal**, v. 51, n. 3, p. 341-351, 2007.

ILLIPRONTI, R. A. et al. Time of pod set and seed position on the plant contribute to variation in quality of seeds within soybean seed lots. **Netherlands Journal of Agricultural Science**, v. 48, p. 165-180, 2000.

ISHIBASHI, Y. et al. Regulation of soybean seed germination through ethylene production in response to reactive oxygen species. **Annals Botany**, v. 111, n. 1, p. 95-102, 2013.

JIA, H.; SUZUKI, M.; McCARTY, D. R. Regulation of the seed to seedling developmental phase transition by the LAFL and VAL transcription factor networks. **Wiley Interdisciplinary Reviews Developmental Biology,** v. 3, n. 1, p. 135-145, 2014.

JONES S. I.; VODKIN, L. O; Using RNA-Seq to profile soybean seed development from fertilization to maturity. **PlosOne,** v. 8, n.3, p. e59270, 2013.

JONES, S. I.; GONZALEZ, D. O.; VODKIN, L. O. Flux of transcript patterns during soybean seed development. **BMC Genomics**, v. 11, p. 136, 2010.

KALEMBA, E. M.; JANOWIAK, F.; PUKACKA, S. Association of Protective Proteins with Dehydration and Desiccation of Orthodox and Recalcitrant Category Seeds of Three Acer Genus Species**. Journal of Plant Growth Regulation**, v. 31, p.351– 362, 2012.

KANE, M. V. et al. Early- maturing soybean cropping system: III. Protein and oil contents and oil composition. **Agronomy Journal**, v. 89, n. 3, p. 464-469, 1997.

KANG, J. et al. Abscisic acid transporters cooperate to control seed germination. **Nature Communications**, v. 6, p. 8113, 2015.

KARSSEN, C. D. et al. Induction of dormancy during seed development by endogenous abscisic acid: Studies of abscisic acid deficient genotypes of *Arabidopsis thaliana* (L.) Heynh. **Planta**, v. 157, p. 158-165, 1983.

KARSSEN, C. M. Hormonal regulation of seed development, dormancy, and germination studied by genetic control. In: KIGEL, J. D.; GALILI, G. (Eds) **Seed development and germination**. New York: Marcel Decker, p. 333-350, 1995.

KAUR, H. et al. Differentially expressed seed aging responsive heat shock protein OsHSP18.2 implicates in seed vigor, longevity and improves germination and seedling establishment under abiotic stress. **Frontiers Plant Science**, v. 6, p. 713, 2015.

KEIRSTEAD, C.H. **Marketing study of factors affecting the quantity and value of products obtained from soybeans**. Washington, DC: United States Departament of Agriculture, Production and Marketing Administration, Fats and Oils Branch, 1952.

KERMODE, A. R. Role of abscisic acid in seed dormancy. **Journal of Plant Growth Regulation**, Berlin, Germany, n. 24, p. 319–344, 2005.

KERMODE, A. R.; BEWLEY, J. D. The role of maturation drying in the transition from seed development to germination: acquisition of desiccation tolerance and germinability during development of *Ricinus communis* L. seeds. **Journal of Experimental Botany**, v. 36, p. 1906-1915, 1985.

KERMODE, A.R. Regulatory mechanisms involved in the transition from seed development to germination. **Critical Reviews in Plant Sciences. v.** 9, p. 155-195, 2990.

KERMODE, A.R.; FINCH-SAVAGE, W. E. Desiccation sensitivity in orthodox and recalcitrant seeds in relation to development. In: Black M, Pritchard HW, editors. **Desiccation and survival in plants: drying without dying**. Wallingford, Oxon: CABI Publishing; 2002. p. 149-184.

KHAN, M. M. et al. Free radical accumulation and lipid peroxidation in testas of rapidly aged soybean seeds: a light-promoted process. **Seed Science Research**, Wallingford, v. 6, n. 3, p. 101-107, 1996.

KOORNNEEF, M.; REULING, G.; KARSSEN, C.M. The isolation and characterization of abscisic acid-insensitive mutants of *Arabidopsis thaliana*. **Physiol Plant**. v. 61, n.3, p.377-383, 1984.

KOTAK, S. et al. A Novel Transcriptional Cascade Regulating Expression of Heat Stress Proteins during Seed Development of *Arabidopsis*. **The Plant Cell**, v. 19, n. 1, p. 182-185, 2007.

KUCERA, B.; COHN, M. A.; LEUBNER-METZGER, G. Plant hormone interactions during seed dormancy release and germination. **Seed Science Research**, n. 15, 281–307, 2005.

LANGMEAD, B. et al. Ultrafast and memory-efficient alignment of short DNA sequences to the human genome. **Genome Biology**, v. 10, n. 3, p.25, 2009.

LARRE, C. et al. Comparative analysis of the heat stable proteome of radicles of *Medicago truncatula* seeds during germination identifies late embryogenesis abundant proteins associated with desiccation tolerance. **Plant Physiology,** Rockville, v.140, p.1418-1436, 2006.

LE, B. H. et al. Global analysis of gene activity during Arabidopsis seed development and identification of seed-specific transcription factors. **Proceedings of the National Academy of Sciences**, v. 107, n. 18, p. 8063-8070, 2010.

LE, B. H. et al. Using genomics to study legume seed development. **Plant Physiology,** v. 144, n. 2, p. 562-574, 2007.

LEE, K. P. et al. A seed coat bedding assay shows that RGL2-dependent release of abscisic acid by the endosperm controls embryo growth in Arabidopsis dormant seeds. **Proceedings of the National Academy of Sciences**, v. 107, n. 44, p. 19108-19113, 2010.

LEPINIEC, L. et al. Genetics and biochemistry of seed flavonoids. **Annual Review of Plant Biology**, v. 57, p. 405-430, 2006.

LEPRINCE, O. et al. Respiratory pathways in germinating maize radicles correlated with desiccation tolerance and soluble sugars. **Physiologia Plantarum**. v. 85, n. 4, p.581-588, 1992.

LEPRINCE, O.; BUITINK, J. Desiccation tolerance: from genomics to the field. **Plant Science**, v. 179, n. 6, p. 554-564, 2010.

LEPRINCE, O.; HENDRY G.A.F.; McKERSIE, B.D. The mechanisms of desiccation tolerance in developing seeds.**Seed Science Research**, v.3, p.231-246, 1993.

LIBAULT, M. et al. An integrated transcriptome atlas of the crop model *Glycine max*, and its use in comparative analyses in plants. **The Plant Journal**, v. 63, p. 86-99, 2010.

LINDQUIST, S.; CRAIG, E. The heat-shock proteins. **Annual Reviews Genet.** n. 22, p. 631-677, 1988.

LISSO, J.; ALTMANN, T.; MÜSSIG, C. The AtNFXL1 gene encodes a NF-X1 type zinc finger protein required for growth under salt stress. **FEBS Letters**, v. 580, n. 20, p. 4851-4856, 2006.

LIU, B. et al. Effects of enhanced UV-B radiation on seed growth characteristics and yield components in soybean. **Field Crops Research,** v. 154, p, 158-163, 2013.

LIU, B. et al. Endogenous hormones in seed, leaf, and pod wall and their relationship to seed filling in soybeans. **Crop &Pasture Science**, v. 61, p. 103–110, 2010.

LIU, B. et al. Genetic redundancy in soybean photoresponses associated with duplication of the phytochrome A gene. **Genetics**, v. 180, p. 995-1007, 2008.

LIU, X. et al. Auxin controls seed dormancy through stimulation of abscisic acid signaling by inducing ARF-mediated ABI3 activation in Arabidopsis. **Proceedings of the National Academy of Sciences**, v. 110, n. 38, p. 15485-15490, 2013.

LIVAK, K. J.; SCHMITTGEN, T. D. Analysis of relative gene expression data using real-time quantitative PCR and the 2 -ΔΔCt Method. **Methods**, v. 25, p. 402-408, 2001.

LONG, S. R., DALE, R. M., SUSSEX, I. M. Maturation and germination of *Phaseolus vulgaris* embryonic axes in culture. **Planta**, v. 153, p. 405-415, 1981.

LOVE, M. I.; HUBER, W.; ANDERS, S. Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. **Genome Biology**, v. 15, p. 550, 2014.

MA, L. et al. Simultaneous determination of 15 plant growth regulators in bean sprout and tomato with liquid chromatography-triple quadrupole tandem mass spectrometry. **Food Analytical Methods**, v. 6, p. 941-951, 2013.

MACOVEI, A. et al. New insights on the barrel medic *MtOGG1* and *MtFPG* functions in relation to oxidative stress response in planta and during seed imbibition. **Plant Physiology and Biochemistry,** v. 49, n. 9, p. 1040–1050, 2011.

MAEO, K. et al. An AP2-type transcription factor, WRINKLED1, of *Arabidopsis thaliana* binds to the AW-box sequence conserved among proximal upstream regions of genes involved in fatty acid synthesis. **The Plant Journal**, v. 60, n. 3, p. 476-487, 2009.

MAO, Z.; SUN, W. Arabidopsis seed-specific vacuolar aquaporins are involved in maintaining seed longevity under the control of ABSCISIC ACID INSENSITIVE. **Journal of Experimental Botany**, v. 66, p. 4781-4794, 2015. doi:10.1093/jxb/erv244.

MARCOS FILHO, J. **Fisiologia de sementes de plantas cultivadas**. Piracicaba: FEALQ, 2005. 495 p.

MATILLA, A. J.; MATILLA-VAZQUEZ, M. A. *Involvement of ethylene in seed physiology*. **Plant Science**, v. 175**, p. 87-98, 2008.**

MAY, M. J. et al. Glutathione homeostasis in plants: implications for environmental sensing and plant development. **Journal Experimental Botany**, v. 49, n. 321, p. 649-667, 1998.

MCDONALD, M.B. 1999. Seed deterioration: physiology, repair and assessment. **Seed Science Technology**. v. 27, p. 177-237, 1999.
McWILLIAMS, D. A.; BERGLUND, D. R.; ENDRES, G. J. **Soybean Growth and Management**. North Dakota State University, 1999.

MEDIC, J.; ATKINSON, C.; HURBURGH JR., C., R. Current Knowledge in Soybean Composition. Journal of the American Oil Chemists Society, v. 91, n. 3, p. 363-384, 2014.

MERTZ, L.M.; HENNING, F.A.; CRUZ, H.L.; MENEGHELLO, G.E.; FERRARI, C.S.; ZIMMER, P.D. Diferenças estruturais entre tegumentos de sementes de soja com permeabilidade contrastante. **Revista Brasileira de Sementes**, v.31, n.1, p.23-29, 2009.

MISRA, S.; BEWLEY, J. D. Reprogramming of protein synthesis from a developmental to a germinative mode induced by desiccation of the axes of *Phaseolus vulgaris*. **Plant Physiology,** v. 78, p. 876-882, 1985.

MITTLERA, R. Oxidative stress, antioxidants and stress tolerance. **Trends in Plant Science,** Oxford, v. 7, n. 9, p. 405-410, 2002.

MORALES, M. A. P. et al. Transcriptome analyses and virus induced gene silencing identify genes in the *Rpp4*-mediated Asian soybean rust resistance pathway. **Functional Plant Biology**, v. 40, n.10, p. 1029-1-47, 2013.

MUDGE, J. et al. Highly syntenic regions in the genomes of soybean, *Medicago truncatula*, and *Arabidopsis thaliana*. **BMC Plant Biology**. v. 5, n.15, 2005.

NAGAO, R. T. et al. Analysis of multiple classes of soybean heat shock genes and proteins. p. 3–20. Physical stresses in plants: Genes and their products for tolerance. *In:* Biochemical and Cellular Mechanisms of Stress Tolerance in Plants: Proc. of the NATO Advanced Research Workshop, Maratea, Italy. 20–24 June 1994. Springer-Verlag, Berlin

NAKABAYASHI, K. et al. Genome-wide profiling of stored mRNA in Arabidopsis thaliana seed germination: epigenetic and genetic regulation of transcription in seed. **The Plant Journal**, v. 41, p. 697-709, 2005.

NAKAJIMA, S. et al. Chlorophyll *b* Reductase Plays an Essential Role in Maturation and Storability of Arabidopsis Seeds. Plant Physiology, v. 160, n. 1, p. 261–273, 2012.

NAMBARA, E.; MARION-POLL, A. ABA action and interactions in seeds. **Trends in Plant Science**, v. 8, n. 5, p. 213-217, 2003.

NAMBARA, E.; MARION-POLL, A. Abscisic acid biosynthesis and catabolim. **Annual Review Plant Biologist,** v. 56, p. 165-185, 2005.

NONOGAKI, H.; BASSEL, G. W.; BEWLEY, J. D. Germination: still a mystery. **Plant Science**, v. 179, n. 6, p. 574-581, 2010.

OBENDORF, R. L. et al. Accumulation of soluble carbohydrates during seed development and maturation of low-raffinose, low-stachyose soybean. **Crop Science**, v. 49, p. 329-341, 2009.

OBENDORF, R. L. et al. Influence of seed maturation on germinability in soybean. **Crop Science**, v. 20, p. 483-486, 1980.

OBENDORF, R. L. et al. Soluble oligosaccharides and galactosyl cyclitols in maturing soybean seeds in planta and in vitro. **Crop Science**, v. 38, p. 78-84, 1998.

OGÉ, L. et al. Protein Repair L-Isoaspartyl Methyltransferase1 is involved in both seed longevity and germination vigor in Arabidopsis. **The Cell Plant**, v. 10, n. 11, p. 3022-3037, 2008.

OKAMOTO, M. et al. CYP707A1 and CYP707A2, which encode abscisic acid 8'-hydroxylases, are indispensable for proper control of seed dormancy and germination in Arabidopsis. **Plant Physiology**, v. 141, n. 1, p. 97–107, 2006.

OOMS, J. et al. Acquisition of Desiccation Tolerance and Longevity in Seeds of Arabidopsis thaliana (A Comparative Study Using Abscisic Acid-Insensitive abi3 Mutants). **Plant Physiology**, v. 102, n. 4, p. 1185-1191, 1993.

ORNBOS Jr, D. L. Production environment and seed quality. p 119-152. In: Barsa, A.S., ed. **Seed Quality: Basic Mechanisms and Agricultural Implications**. Food Products Press, New York, NY, USA, 1995.

PÁDUA, G. P. et al. Incidence of green soybean seeds as a function of environmental stresses during seed maturation. **Revista Brasileira de Sementes**, v. 31, n. 3, p. 150–159, 2009.

PÁDUA, G. P. et al. Tolerance level of green seed in soybean seed lots after storage. **Revista Brasileira de Sementes**, v. 29, n. 3, p. 112–20, 2007.

PÁDUA, G. P. et al. Zoneamento agroclimático do estado de Minas Gerais para a produção de semente de soja de alta qualidade. **Journal of Seed Science**, Londrina, v. 36, n. 4, 2014.

PAMMENTER, N. W.; BERJAK, P. A review of recalcitrant seed physiology in relation to desiccation tolerance mechanisms. **Seed Science Research**, v. 9, n. 1, p.13-37, 1999.

PARCY, F. et al. The *ABSCISIC ACID-lNSENSITIVE3, FUSCA3,* and *LEAFY COTYLEDONf* Loci Act in Concert to Control Multiple Aspects of Arabidopsis Seed Development. **The Plant Cell**, v. 9, p. 1265-1277, 1997.

PELTIER, A.J.; HATFIELD, R.D.; GRAU, C.R. Soybean stem lignin concentration relates to resistance to *Sclerotinia Sclerotiorum*. **Plant Diseases**, v. 93, n. 2, p;149-154, 2009.

PERSONAT, J. M. et al. Co-overexpression of two Heat Shock Factors results in enhanced seed longevity and in synergistic effects on seedling tolerance to severe dehydration and oxidative stress. **BMC Plant Biology**, v. 14, n. 56, 2014.

PFAFFL, M. W.; HORGAN, G. W.; DEMPFLE L. Relative expression software tool (REST©) for group-wise comparison and statistical analysis of relative expression results in real-time PCR. **Nucleic Acids Research**, v. 30, n. 9, 2002.

POPINIGS, F. **Fisiologia da semente.** 2. ed. Brasília: AGIPLAN, 1985. 289p.

POTTERS, G. et al. Ascorbate and glutathione: guardians of the cell cycle, partners in crime? **Plant Physiology and Biochemistry**, v. 40, n. 6-8, p. 537-548, 2002.

PRASAD, B.; PRASAD, R.; PRASAD, S. Seed quality variation in relation to pod and seed position on the mother plant of soybean [*Glycine max*. (L.) Merrill] seed Iot. **Journal of Crop and Weed**. v. 6, n. 2, p.1-5, 2010.

PRATTLEY, C. A.; STANLEY, D. W. Protein-phytate interactions in soybeans. I. Localization of phytate in protein bodies and globoids. **Journal of Food Biochemistry,** v. 6, n. 4, p. 243-253, 1982.

PRIETO-DAPENA, P. et al. Improved Resistance to Controlled Deterioration in Transgenic Seeds. **Plant Physiology,** v. 142, n. 3, p. 1102-1112, 2006.

PROBERT, R. et al. Seed quality for conservation is critically affected by pre-storage factors. **Australian Journal of Botany**, v. 55, p. 326-335, 2007.

QIU, L. J., CHANG, R. Z. The origin and history soybean. In: SINGH, G. (Ed.). **The soybean**: botany, production and uses. Ludhiana: CAB, 2010. p. 13-35.

QUEBEDEAUX, B.; SWEETSER, P. B.; ROWELL, J.C. Abscisic Acid Levels in Soybean Reproductive Structures during Development. **Plant Physiology**, v. 58, n. 3, p. 363-366, 1976.

QUEITSCH, C. et al. Heat shock protein 101 plays a crucial role in thermotolerance in Arabidopsis.**Plant Cell**, v.12, n.4, p.479-492, 2000.

RABOY, V.; DICKINSON, D. B. The timing and rate of phytic acid accumulation in developing soybean seeds. **Plant. Physiology**, v. 85, p. 0841-844. 1987.

RAIJ, B. et al. Recomendações de adubação e calagem para o Estado de São Paulo**.** **Boletim Técnico do Instituto Agronômico de Campinas**, Campinas, n. 100, 1997.

RAJJOU, L. et al. Proteome-wide characterization of seed aging in Arabidopsis. A comparison between artificial and natural aging protocols. **Plant Physiology.** v. 148, p. 620-641, 2008.

RAJJOU, L. et al. Seed germination and vigor. **The Annual Review of Plant Biology**, v. 63, p. 507-533, 2012.

RAJJOU, L. et al. The effect ofα-amanitin on the Arabidopsis seed proteome highlights the distinct roles of stored and neosynthesized mRNA during germination. **Plant Physiology**, v. 134, p. 1518-1613, 2004.

RAJJOU, L.; DEBEAUJON, I. Seed longevity: survival and maintenance of high germination ability of dry seeds. ***Comptes Rendus Biologies***, v. 331, n. 10, p. 796–805, 2008.

RANATHUNGE, K. et al. Properties of the soybean seed coat cuticle change during development. **Planta**, v. 231, n. 5, p. 1171-1188, 2010.

REN, C.; BILYEN, K. D.; BEUSELINCK, P. R. Composition, vigor and proteome of mature soybean seeds developed under high temperature. **Crop Science**, v. 49, p. 1010-1022, 2009.

RIGHETTI, K. et al. Inference of longevity-related genes from a robust coexpression network of seed maturation identifies regulators linking seed storability to biotic defense-related pathways. **The Plant Cell**, v. 27, p. 2692-2708, 2015.

RITCHIE, S. W.; HANWAY, J. J.; THOMPSON, H. E. How a soybean plant develops. Cidade: Iowa State University of Science and Technology, 1982. (Special Report, 53).

ROSENBERG, L. A.; RINNE, R. W. Moisture loss as a prerequisite for seedling growth in soybean seeds (*Glycine max* L. Merr.). **Journal of Experimental Botany**, v. 37, p. 1663-1674, 1986.

RUIJTER, J. M. et al. Evaluation of qPCR curve analysis methods for reliable biomarker discovery: Bias, resolution, precision, and implications. **Science Direct Methods**, v. 59, n. 1, p. 32-46, 2013.

RUSHTON, P. J. et al. WRKY transcription factors. **Trends in Plant Science**, v. 15, n. 5, p. 247-258, 2010.

RYLOTT, E.L.; GILDAY, A.D., GRAHAM, L.A. The gluconeogenic enzyme phospho*enol*pyruvate carboxykinase in arabidopsis is essential for seedling establishment. **Plant Physiology.** v. 131, n. 4, p.1834-1842, 2003.

SALDIVAR, X. et al. Changes in chemical composition during soybean seed development. **Food Chemistry**, v. 124, n. 4, p. 1369-1375, 2011.

SAMARAH, N. H. et al. Ethylene evolution from soybean seeds podded and depodded related to seed desiccation tolerance during maturation**. Seed Science and Technology.** v. 44, n. 1, p. 53-63, 2016.

SANDOVAL, J. A. et al. N-Acylphosphatidylethanolamine in dry and imbibing cotton seeds: amounts, molecular species, and enzymatic synthesis. **Plant Physiology**, v. 109, n. 1, p. 269-275, 1995.

SANHEWE, A. J.; ELLIS, R. H. Seed development and maturation in *Phaseolus vulgaris* II. Post-harvest longevity in air-dry storage. **Journal Experimental Botany**, v. 7, n. 7, p. 959-965, 1996.

SANO, N. et al. Staying alive: molecular aspects of seed longevity. **Plant and Cell Physiology**, p. 1-15, 2015.

SANTOS, E. L. et al. Qualidade fisiológica e composição química das sementes de soja com variação na cor do tegumento. **Revista Brasileira de Sementes**, v. 29, n. 1, p. 20-26, 2007.

SANTOS, T. L. Soja. In: CASTRO, P. R. C.; KLUGE, R. A.; SESTARI, I. **Manual de fisiologia vegetal: fisiologia dos cultivos.** Piracicaba: Editora Agronômica Ceres, p. 157-175, 2008.

SANTOS-MENDOZA, M. et al. LEAFY COTYLEDON 2 activation is sufficient to trigger the accumulation of oil and seed specific mRNAs in Arabidopsis leaves. **FEBS Letters**, v. 579, n. 21, p. 4666-4670, 2005.

SCANDALIOS, J. G. Oxygen stress and superoxide dismutases. **Plant Physiology**, Bethesda, v. 101, n. 1, p. 7-12, 1993.

SCHMUTZ J. et al. Genome sequence of the palaeopolyploid soybean. **Nature.** v. 463, p. 178-183, 2010.

SCHUSSLER, J. R., BRENNER, M. L., BRUN, W. A. Abscisic acid and its relationship to seed filling in soybeans. **Plant Physiology**, v. 76, p. 301-306, 1984.

SCOFIELD, S.; MURRAY, J. A. KNOX gene function in plant stem cell niches. **Plant Molecular Biology**, v. 60, n. 6, p. 929-946, 2006.

SEDIYAMA, T.; PEREIRA, M. G.; SEDIYAMA, C. S.; GOMES, J. L. L. **Cultura da Soja, Parte I**. Viçosa: UFV, p.97, 1993.

SEVERIN, A. J. et al. RNA-Seq Atlas of Glycine max: A guide to the soybean transcriptome. **BioMed Central Plant Biology**, v. 10, n. 160, 2010.

SEVERIN, A. J. et al. RNA-Seq Atlas of Glycine max: A guide to the soybean transcriptome. **BioMed Central Plant Biology**, v. 10, n. 160, p. 1-16, 2010.

SHA, A. H. et al. Large-scale sequencing of normalized full-length cDNA library of soybean seed at different developmental stages and analysis of the gene expression profiles based on ESTs. **Molecular Biology Reports**, v. 39, n. 3, p. 2867-2874, 2012.

SHAMIMUZZAMAN, M.; VODKIN, L. Identification of soybean seed developmental stage-specific and tissue-specific miRNA targets by degradome sequencing. **BMC Genomics**, v. 13, p. 310, 2012.

SHARMA, S. et al. Positional effects on soybean seed composition during storage, **J Food Sci Technol,** v. 2, n. 50, p. 353-359, 2013.

SINNECKER, P. Degradação da clorofila durante a maturação e secagem de semente de soja. 2002. 103 p. **Tese** (Doutorado em Ciência dos Alimentos)-Faculdade de Ciências Farmacêuticas, Universidade de São Paulo, São Paulo, 2002.

SOUZA, F. H. D.; MARCOS-FILHO, J. The seed coat as a modulator of seed-environment relationships in Fabaceae. **Revista Brasileira de Botânica,** v. 24, n.4. p. 365-375, 2001.

SU, T. et al. WRKY42 Modulates Phosphate Homeostasis through Regulating Phosphate Translocation and Acquisition in Arabidopsis. **Plant Physiology**, v. 167, n. 4, p. 1579-1591, 2015.

SUN, W. O.; LEOPOLD, A. D. Acquisition of desiccation tolerance in soybeans. **Physiologia Plantarium**, v. 87, p. 403-409, 1993.

TAIZ, L.; ZEIGER, E. **Fisiologia Vegetal**. 5. ed. São Paulo: Artmed, 2013. 918p.

TEIXEIRA, R. N. et al. Gene expression profiling of the green seed problem in Soybean. **BioMed Central Plant Biology**, v. 16, n. 37, p. 1-15, 2016.

TEJEDOR-CANO, J. et al. Loss of function of the HSFA9 seed longevity program. **Plant, Cell & Environment,** v. 33, n. 8, p. 1408-1417, 2010.

TEKRONY, D. M. et al. Effect of field weathering on the viability and vigour of soybean seed. **Agronomy Journal**, v. 72, p. 749-753, 1980.

TEKRONY, D. M. et al. Physiological maturity in soybean. **Agronomy Journal**, v. 71, p. 771-775, 1979.

TO, A. et al. A Network of Local and Redundant Gene Regulation Governs *Arabidopsis* Seed Maturation. **The Plant Cell**, v. 18, p. 1642-1651, 2006.

TSUCHIYA et al. The FUS3 transcription factor functions through the epidermal regulator TTG1 during embryogenesis in Arabidopsis. **Plant Journal**, v. 37, n.1, p. 73-81, 2004.

TUNNACLIFFE, A.; WISE, M. The continuing conundrum of the LEA proteins..**The Science of Nature**. v. 94, n. 10, p. 791-812, 2007.

VANDENABEELE, J. D. S. et al. Dual action of the active oxigen species during plant stress responses. **Cellular and Molecular Life Science**, Basel, v. 57, n. 5, p. 779-795, 2000.

VERDIER, J. et al. A regulatory network-based approach dissects late maturation processes related to the acquisition of desiccation tolerance and longevity of *Medicago truncatula* seeds. **Plant Physiology**, v. 163, p. 757-774, 2013.
VERTUCCI, C.W.; FARRANT, J. M. Acquisition and loss of desiccation tolerance. In: KIGEL, J.; GALILI, G. (Ed.). S**eed development and germination**. New York: Marcel Dekker, 1995. p.237-271.

VICENTE-CARBAJOSA, J. et al. Barley BLZ1: a bZIP transcriptional activator that interacts with endosperm-specific gene promoters. **The Plant Journal**, v. 13, n. 5, p. 629-640, 1998.

VICENTE-CARBAJOSA, J.; CARBONERO, P. Seed maturation: developing an intrusive phase to accomplish a quiescent state. **International Journal of Developmental Biology**, v. 49, n. 5-6, p. 645-651, 2005.
WALTERS, C. et al. Preservation of recalcitrant seeds. **Science**. v. 339, p. 915-916, 2013.

WAN, Y. et al. The signal transducer NPH3 integrates the phototropin1 photosensor with PIN2-based polar auxin transport in arabidopsis root phototropism. **The Plant Cell**. v. 24, p.551-565, 2012.

WANG, W.X.; VINOCUR, B.; ALTMAN,A. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. **Planta**. v.218, n.1, p.1-14, 2003.

WATANABE, I.; NAGASAWA, T. Appearance and chemical composition of soybean seeds in germplasm collection of Japan: II. Correlation among protein, lipid and carbohydrate percentage. **Japanese Journal of Crop Science**, v. 59, p. 661–666, 1990.

WATERWORTH, W. M. et al. A plant DNA ligase is an important determinant of seed longevity. **The Plant Journal**, v. 63, n. 5, p. 848-860, 2010.

WEHMEYER, N.; VIERLING, E. The expression of small heat shock proteins in seeds responds to discrete developmental signals and suggests a general protective role in desiccation tolerance. **Plant Physiology**, v. 1226, n. 1, p. 1099-1108, 2000.

WEITBRECHT, K.; KERSTIN MÜLLER, K.; LEUBNER-METZGER, G. First off the mark: early seed germination. **Journal of Experimental Botany**, v. 62, n. 10, p. 3289-3309, 2011.

WHITE, C.N.; RIVIN, C.J. Gibberellins and seed development in maize. II. Gibberellin synthesis inhibition enhances abscisic acid signaling in cultured embryos. **Plant Physiol.** v. 122, n. 4, p.1089-97, 2000.

WHITEHOUSE, K. J.; HAY, F. R; ELLIS, R. H. Increases in the longevity of desiccation-phase developing rice seeds: response to high-temperature drying depends on harvest moisture content. **Annals of Botany**, v. 117, n. 5, p. 1-13, 2016.

WILLARD, C. J. The time of harvesting soybeans for hay and seed. **Journal of the American Society of Agronomy**, v. 17, n. 2, p. 157-168, 1925.

WILSON, R. F. **Seed composition Soybeans**: Improvement, production and users. 3rd. ed. Madison, WI. : ASA, CSSA, SSSA, 2004.

WISE, M. J. LEAping to conclusions: A computational reanalysis of late embryogenesis abundant proteins and their possible roles. **BMC Bioinformatics**. v. 4, n. 1, p. 52-54, 2003.

XU, N.; BEWLEY, J. D. Sensitivity to abscisic acid and osmoticum changes during embryogenesis of alfafa (*Medicago Sativa*). **Journal of Expimental Botany**, v. 42, n. 6, p. 821-826, 1991.

XUE-FEI, D. et al. The SnRK protein kinase family and the function of SnRK1 protein kinase. **International Journal of Agriculture & Biology,** v. 14, n. 4, p. 575-579, 2012.

YI, X.; DU, Z.; SU, Z. PlantGSEA: a gene set enrichment analysis toolkit for plant community. **Nucleic Acids Research**. v. 41, W98–103. 2013.

ZANAKIS, G. N.; ELLIS, R. H.; SUMMERFIELD, R. J. Seed quality in relation to seed development and maturation in three genotypes of soybean (*Glycine max*). **Experimental Agriculture.** v. 30, p. 139-156, 1994.

ZENTELLA, R.; YAMAUCHI, D.; HO, T. H. D. Molecular dissection of the gibberellin/abscisic acid signaling pathways by transiently expressed RNA interference in Barley aleurone cells. **Plant Cell**. Rockville, v. 14, p. 2289-2301, 2002.

ZORATTO, M. F. et al. Presença de sementes esverdeadas em soja e seus efeitos sobre seu potencial fisiológico. **Revista Brasileira de Sementes,** v.29, n. 1, p. 11–7, 2009.