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LSD 3.0: a comprehensive resource for the leaf senescence research community

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ABSTRACT

The leaf senescence database (LSD) is a comprehensive resource of senescence-associated genes (*SAG*s) and their corresponding mutants. Through manual curation and extensive annotation, we updated the LSD to a new version LSD 3.0, which contains 5853 genes and 617 mutants from 68 species. To provide sustainable and reliable services for the plant research community, LSD 3.0 (https://bigd.big.ac.cn/lsd/) has been moved to and maintained by the National Genomics Data Center at Beijing Institute of Genomics, Chinese Academy of Sciences. In the current release, we added some new features: (i) Transcriptome data of leaf senescence in poplar were integrated; (ii) Leaf senescence-associated transcriptome data information in *Arabidopsis*, rice and soybean were included; (iii) Senescence-differentially expressed small RNAs (Sen-smRNA) in *Arabidopsis* were identified; (iv) Interaction pairs between Sen-smRNAs and senescence-associated transcription factors (Sen-TF) were established; (v) Senescence phenotypes of 90 natural accessions (ecotypes) and 42 images of ecotypes in *Arabidopsis* were incorporated; (vi) Mutant seed information of *SAG*s in rice obtained from Kitbase was integrated; (vii) New options of search engines for ecotypes and transcriptome data were implemented. Together, the updated database bears great utility to continue to provide users with useful resources for studies of leaf senescence.

INTRODUCTION

Plant leaves harvest light energy and fix CO_2 to produce carbohydrates, and serve as a major food source on the earth (1). The leaf undergoes complex developmental and physiological transitions during their life history. Senescence is the final stage of leaf lifespan and is essential for plant fitness as nutrient remobilization from senescing leaves to developing organs through this process (2–4). Therefore, leaf senescence has been regarded as a genetically controlled biological process that was evolutionarily acquired for better fitness and survival (5). Efforts to understand the molecular regulatory mechanisms underlying leaf senescence have been largely made by genetic, genomic, transcriptomic, proteomic and metabolomic studies, revealing that leaf senescence is a highly coordinated process regulated by a large number of senescence-associated genes (*SAG*s) (5). Forward genetic studies of leaf senescence by screening senescence-related mutants and reverse genetic analyses of *SAG*s in plants have provided deep insights into the molecular basis of leaf senescence (6). To facilitate systematic and comparative studies of leaf senescence, we developed the leaf senescence database (LSD) in 2010 and updated to LSD 2.0 in 2014 with 5356 genes and 324 mutants from 44 species (7,8). These *SAG*s were manually retrieved based on experimental evidence and were categorized according to their functions in leaf senescence. We performed extensive curations through both manual and computational approaches to provide comprehensive annotations for *SAG*s. Currently,

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LSD has been widely used for functional studies of *SAG*s in *Arabidopsis* and systematic identification of *SAG*s in agronomically important plants (9–13).

In the past five years, continuously increasing efforts have been devoted to the field of leaf senescence studies, accordingly leading to the identification of a number of genes as functional *SAG*s. For example, circadian clock genes, such as *EARLY FLOWERING 3* (*ELF3*), *EARLY FLOWERING 4* (*ELF4*), *LUX ARRHYTHMO* (*LUX*) and *PSEUDO-RESPONSE REGULATOR 9* (*PRR9*), affect both dark-induced and age-dependent leaf senescence (14,15). Specifically, *PRR9* promotes leaf senescence through directly transcriptional activation of *ORESARA1* (*ORE1*), an important positive regulator of senescence (16,17), and indirectly via suppressing *miR164*, a post-transcriptional repressor of *ORE1*. Recently, epigenetic regulation pathways have been found to be involved in regulating the leaf senescence process (18). The histone H3K4 demethylase *JMJ16* negatively regulates age-dependent leaf senescence, and loss-of-function of *JMJ16* increases H3K4me3 levels and induces the expression of numerous *SAG*s (13). The H3K27me3 demethylase REF6 positively regulates senescence process by directly upregulating *SAG*s, such as *ETHYLENE INSENSITIVE 2* (*EIN2*) and *ORE1* (19). Reverse genetic studies have also revealed that several senescence-associated transcription factors (Sen-TFs), for example, *WRKY75*, *ANAC019*, *ANAC032*, *ANAC072* and *OsNAC2*, function as positive regulators of leaf senescence (11,20,21). The ABA receptor *PYRABACTIN RESISTANCE 1-LIKE 9* (*PYL9*) accelerates leaf senescence but promotes extreme drought tolerance in *Arabidopsis* (22). Moreover, high-resolution time-course transcriptome analyses in *Arabidopsis* identified a large number of new *SAG*s (23) through small RNA-TF regulatory networks (24), especially miRNAs and transacting small interfering RNAs (tasiRNAs), providing new insights into the fine regulation of leaf senescence process.

To cover the important progress achieved in the past several years and extend the web functionality of LSD, we upgraded it to a new version LSD 3.0 by extensive manual curation and annotation. LSD 3.0 integrates a comprehensive collection of 5853 genes and 617 mutants from 68 species (Table 1 and Supplementary Table S1), an extension from LSD 2.0 containing 5356 genes and 322 mutants from 44 species. To facilitate comparative study of the molecular regulatory mechanisms of leaf senescence in perennial and annual plants, we identified 678 *SAG*s in poplar leaves by high-resolution temporal transcriptome analysis of autumn leaf senescence. New features were included in the current version, including images of *Arabidopsis* ecotypes, senescence differentially expressed small RNAs (DEsmRNA), DEsmRNA–SenTFs interaction pairs, and implementation of new options of search engines for ecotypes and transcriptome data.

NEW FEATURES

Data collection

We collected all *SAG*s and mutants from published papers from January 2014 to April 2019 by searching the PubMed literature database with keywords 'leaf senescence', 'leaf & senescence', 'plant senescence' and 'plant aging', respectively. Then, we performed manual curation to retrieve a wide range of information, including gene name, locus name, GenBank ID, PubMed ID, mutant, species, senescence-associated phenotypes, the effect on leaf senescence and evidence. At last, we made extensive annotations for these *SAG*s through computational approaches (8).

Database access

To provide sustainable and reliable services to the plant leaf senescence research community, the website of LSD 3.0 has been moved to and maintained by the National Genomics Data Center (formerly named as BIG Data Center) (25) at Beijing Institute of Genomics, Chinese Academy of Sciences, and is publicly available at https://bigd.big.ac.cn/lsd/. Users can browse, search and download all the data through friendly web interfaces. A tree-like structure was designed for both species and phenotypes, and tables were also used to organize all relevant information for species, mutants, QTL, ecotypes, *Arabidopsis* and rice seeds, sen-smRNA, poplar transcriptome and public transcriptome data obtained from the GEO database (https://www.ncbi.nlm.nih.gov/geo/). In addition, the text search interface was updated and improved by allowing users to perform six types of queries: (i) GenBank ID, species, effects and description of genes; (ii) name and ecotype of mutants; (iii) title, author, journal and date of literature papers; (iv) locus name, alias and keywords; (v) miRNA name and (vi) locus name of poplar transcriptome.

Example of annotation

LSD 3.0 features comprehensive collection and extensive annotations of *SAG*s. A typical example is *NOE1* (LOC_Os03g03910) encoding a rice catalase. Loss-of-function of *NOE1* promotes leaf senescence by increasing the production of H_2O_2 in the leaves (26). Accordingly, the current release of LSD provided a wealth of information for *NOE1* obtained by both manual and computational approaches (Figure 1). We performed detailed annotations and organized all relevant information in terms of basic information (locus name, organism, function category, effect for senescence, evidence, references, protein–protein interactions and sequence) (Figure 1A), mutant information (Figure 1B), miRNA interaction (Figure 1C), ortholog group (Figure 1D), cross link (Figure 1E) as well as newly added mutant seed information (Figure 1F).

Transcriptome data of leaf senescence in Poplar

At present, thousands of *SAG*s have been identified and functionally studied in annual plants such as *Arabidopsis*, rice, maize or sorghum (5), while fewer *SAG*s have been identified in perennial woody plants due to the lack of well-annotated whole genomes (27). Poplar (*Populus trichocarpa*) is the first sequenced genome of the forest tree because of its modest genome size, rapid growth rate and relative ease of experimental manipulation (27). To provide the transcriptomic picture of leaf senescence in perennial

Table 1. Statistics and comparisons of gene number among the three versions of LSD

Species	LSD 1.0	LSD 2.0	LSD 3.0
Grain Amaranths (*Amaranthus hypochondriacus*)	0	1	1
Arabidopsis lyrata	0	2	2
Arabidopsis thaliana	949	3744	3852
Chinese Milk Vetch (*Astragalus sinicus*)	1	1	1
Birch (*Betula pendula*)	0	0	1
Cabbage (*Brassica campestris*)	0	2	2
Rapeseed (*Brassica napus*)	15	8	13
Broccoli (*Brassica oleracea*)	4	9	9
Turnip (*Brassica rapa*)	0	0	1
Chinese cabbage (*Brassica rapa subsp. Pekinensis*)	0	1	1
Cabbage (*Brassica rapa var. parachinensis*)	0	5	19
Tea (*Camellia sinensis*)	0	1	3
Pepper (*Capsicum annuum*)	0	1	3
Red goosefoot (*Chenopodium rubrum*)	1	1	1
Chrysanthemum (*Chrysanthemum morifolium*)	0	0	1
Sweet Orange (*Citrus sinensis*)	0	0	4
Autumn Crocus (*Crocus sativus*)	0	1	1
Muskmelon (*Cucumis melo*)	0	1	1
Carrot (*Daucus carota*)	0	1	1
Carnation (*Dianthus caryophyllus*)	0	1	1
Persimmon (*Diospyros kaki*)	0	0	2
Erianthus arundinaceus	0	0	1
Tall fescue (*Festuca arundinacea*)	0	1	1
Fescue (*Festuca pratensis Huds*)	1	1	1
Strawberry (*Fragaria x ananassa*)	0	1	1
Soybean (*Glycine max*)	4	12	20
Cotton (*Gossypium hirsutum*)	0	0	15
Sunflower (*Helianthus annuus*)	0	0	5
Barley (*Hordeum vulgare*)	3	14	19
Sweet potato (*Ipomoea batatas*)	0	4	8
Japanese morning glory (*Ipomoea nil*)	1	1	2
Physic nut (*Jatropha curcas*)	0	0	1
Easter lily (*Lilium longiflorum*)	0	0	1
Litchi trees (*Litchi chinensis*)	0	0	1
Perennial ryegrass (*Lolium perenne*)	0	4	5
Apple (*Malus domestica*)	0	0	3
Chinese crabapple (*Malus prunifolia*)	0	0	2
Mango (*Mangifera indica*)	0	1	1
Alfalfa (*Medicago sativa*)	1	2	3
Medicago truncatula	31	31	31
Miscanthus lutarioriparius	0	0	11
Mulberry (*Morus alba*)	0	0	1
Banana (*Musa acuminata*)	0	882	882
Banana (*Musa x paradisiaca*)	0	0	1
Bamboo (*Neosinocalamus affinis*)	0	1	1
Coyote tobacco (*Nicotiana attenuata*)	0	1	1
Tobacco (*Nicotiana tabacum*)	5	9	18
Rice (*Oryza sativa*)	104	132	188
Petunia (*Petunia hybrida*)	0	1	1
Picrorhiza (*Picrorhiza kurrooa Royle ex Benth*)	0	0	1
Pea (*Pisum sativum*)	4	6	6
Balloon flower (*Platycodon grandiflorum*)	0	1	1
Poplar (*Populus tremula x Populus tremuloides*)	0	0	198
Poplar (*Populus trichocarpa*)	0	0	1
Peach (*Prunus persica L. Batsch*)	0	0	1
Pear (*Pyrus communis*)	0	0	1
Radish (*Raphanus sativus*)	0	0	1
Rose (*Rosa hybrida*)	1	1	1
Foxtail millet (*Setaria italica*)	0	0	2
Tomato (*Solanum lycopersicon*)	8	23	37
Potato (*Solanum tuberosum*)	3	3	6
Sorghum (*Sorghum bicolor*)	4	26	26
Spinach (*Spinacia oleracea*)	0	2	2
Sugarcane	0	0	1
Wheat (*Triticum aestivum*)	1	256	259
Wheat (*Triticum turgidum*)	1	65	65
Cowpea (*Vigna unguiculata*)	0	1	1
Maize (*Zea mays*)	3	94	98
Total 68	1145	5356	5853

A **Basic information**

Locus name	LOC_Os03g03910
Alias	NOE1
Organism	Rice (*Oryza sativa*)
Taxonomic identifier	[NCBI]
Function category	Redox regulation
Effect for Senescence	promote
Gene Description	nitric oxide excess1 (noe1)
Evidence	Genetic evidence:Mutant [Ref 1]
References	1: Lin A, Wang Y, Tang J, Xue P, Li C, Liu L, Hu B, Yang F, Loake GJ, Chu C Nitric oxide and protein S-nitrosylation are integral to hydrogen peroxide-induced leaf cell death in rice. Plant Physiol. 2012 Jan;158(1):451-64 2: Wang Y, Lin A, Loake GJ, Chu C H2O2-induced leaf cell death and the crosstalk of reactive nitric/oxygen species. J Integr Plant Biol 2013 Mar;55(3):202-8
Gene Ontology	**biological process**: oxidation-reduction process; response to oxidative stress **molecular function**: catalase activity; heme binding
Pathway	**KEGG**: map00380 (EC 1.11.1.6); map00680 (EC 1.11.1.6) **MetaCyc**: PWY-5506
Sequence	LOC_Os03g03910.1 | Genomic | mRNA | CDS | Protein

B **Mutant information**

Mutant name	noe1
Mutant/Transgenic	mutant
Ecotype	Rice (Oryza sativa)
Mutagenesis type	T-DNA insertion_knock out

C **miRNA Interaction**

Details

```
target: LOC_Os03g03910.1
miRNA: osa-miR5543
miRNA: osa-miR5543
mfe: -25.9 kcal/mol
p-value: 0.000000

position: 1651
target 5' A       G            G 3'
           GGGGAGA GUACCGUUCAUG
           UUCUUUU UAUGGUAAGUAU
miRNA  3' G       A              5'
```

D **Ortholog Group**

Ortholog Groups: OG5_127182

Accession	Taxon
NP_001031072	Arabidopsis thaliana
NP_001031073	Arabidopsis thaliana
NP_001031791	Arabidopsis thaliana
NP_195235	Arabidopsis thaliana
NP_564120	Arabidopsis thaliana
NP_564121	Arabidopsis thaliana
NP_973873	Arabidopsis thaliana
CMI050C	Cyanidioschyzon merolae strain 10D
150104	Chlamydomonas reinhardtii
NP_001045673	Oryza sativa Japonica Group
NP_001048861 (LOC_Os03g03910)	Oryza sativa Japonica Group
NP_001058635	Oryza sativa Japonica Group
e_gw1.3.315.1	Physcomitrella patens subsp. patens
estExt_Genewise1.C_2590045	Physcomitrella patens subsp. patens
estExt_Genewise1.C_4220004	Physcomitrella patens subsp. patens
estExt_gwp_gw1.C_2920023	Physcomitrella patens subsp. patens
fgenesh1_pg.scaffold_223000044	Physcomitrella patens subsp. patens
fgenesh1_pg.scaffold_3000179	Physcomitrella patens subsp. patens
gw1.4424.3.1	Physcomitrella patens subsp. patens
29830.m001438	Ricinus communis
30170.m014364	Ricinus communis
XP_002950455	Volvox carteri f. nagariensis

E **Cross Link**

Database	Entry ID	E-value	Start	End	InterPro ID	Description
PIRSF	PIRSF038928	5.7E-203	1	491	IPR024711	Catalase, mono-functional, haem-containing, clades 1 and 3
PANTHER	PTHR11465	1.0E-289	7	489	IPR018028	Catalase, mono-functional, haem-containing
SUPERFAMILY	SSF56634	2.0E-206	13	489	IPR020835	Catalase-like domain
ProSiteProfiles	PS51402	75.1	14	492	IPR018028	Catalase, mono-functional, haem-containing
SMART	SM01060	1.9E-248	18	401	IPR011614	Catalase core domain
Pfam	PF00199	7.0E-182	19	400	IPR011614	Catalase core domain
PRINTS	PR00067	2.1E-81	31	54	IPR018028	Catalase, mono-functional, haem-containing
ProSitePatterns	PS00438	NA	54	70	IPR024708	Catalase active site
PRINTS	PR00067	2.1E-81	94	112	IPR018028	Catalase, mono-functional, haem-containing
PRINTS	PR00067	2.1E-81	115	132	IPR018028	Catalase, mono-functional, haem-containing
PRINTS	PR00067	2.1E-81	134	152	IPR018028	Catalase, mono-functional, haem-containing
PRINTS	PR00067	2.1E-81	299	326	IPR018028	Catalase, mono-functional, haem-containing
PRINTS	PR00067	2.1E-81	331	357	IPR018028	Catalase, mono-functional, haem-containing
ProSitePatterns	PS00437	NA	344	352	IPR002226	Catalase haem-binding site

F

LOC_Os03g03910	FN480-S	Fast-Neutron	Deletion	Chr3:1510660-2364780	Truncation
LOC_Os03g03910	FN701-S	Fast-Neutron	Deletion	Chr3:1781001-1871000	Truncation

Figure 1. A typical entry for the rice *NOE1* gene (LOC_Os03g03910) in LSD 3.0. (**A**) Basic information, (**B**) Mutant information, (**C**) miRNA interaction, (**D**) Ortholog group, (**E**) Cross link to other databases and (**F**) Newly added mutant seed information.

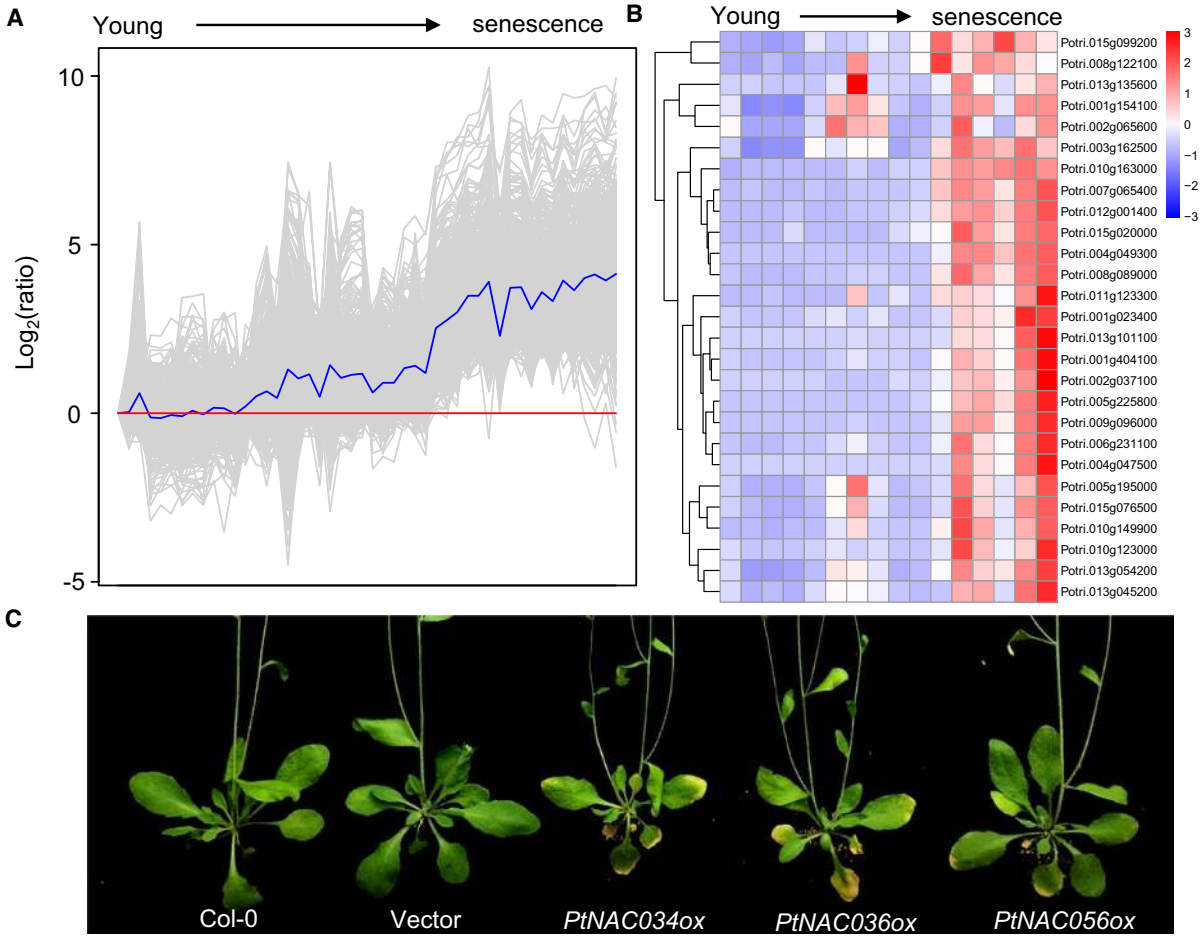

Figure 2. Identification and functional analysis of *SAG*s in poplar. (**A**) Identification of *SAG*s by high-resolution temporal transcriptome of autumn leaf senescence in poplar. (**B**) Heat map showing the expression pattern of several *Sen-TF*s as leaves age in poplar. (**C**) Functional analysis of poplar *Sen-TF*s in *Arabidopsis* reveals that *PtNAC034*, *PtNAC036* and *PtNAC056* positively regulate leaf senescence.

plants, we performed high-resolution time-course profiling of gene expression during autumn leaf senescence in field-grown poplar by RNA sequencing (Figure 2). In total, 678 *SAG*s were identified according to their increased expression levels as leaves age (Figure 2A). Given that leaf senescence is finely tuned by many regulatory factors such as TFs, the senescence-associated TF (*Sen-TF*s) in poplar were identified and functionally characterized (Figure 2B). As shown in Figure 2C, overexpression of three poplar *Sen-TF*s (*PtNAC034*, *PtNAC036* and *PtNAC056*) accelerates leaf senescence process in *Arabidopsis* demonstrated by the earlier leaf yellowing, suggesting that these genes are positive regulators of leaf senescence. Additionally, we identified the senescence-downregulated genes and integrated them in the updated database to provide comprehensive gene expression profiles during autumn leaf senescence.

Newly added annotations

To help researchers study the function of *SAG*s in rice, the mutant seed information obtained from Kitbase (https://kitbase.ucdavis.edu/) was integrated into LSD 3.0. As leaf senescence is influenced by numerous environmental factors such as photoperiod and temperature under natural growth conditions, natural accessions (ecotypes) provide valuable materials to understand the regulatory mechanisms underlying leaf senescence (28,29). To this end, the senescence phenotype information of 90 ecotypes was added in the updated version. High-resolution and multi-dimensional analyses of transcriptome during leaf senescence provide a wealth of information to understand leaf senescence at the molecular level (24). To facilitate researchers to quickly obtain these resources, we searched the relevant transcriptome information from the GEO database (https://www.ncbi.nlm.nih.gov/geo/) and integrated them into LSD 3.0. Given that small RNAs (smRNA) have been demonstrated to be involved in leaf senescence by regulating their target genes, we added the senescence DEsmRNAs as well as DEsmRNA–Sen-TFs interaction pairs into LSD 3.0.

DISCUSSION AND FUTURE DIRECTIONS

In the updated version, we have collected the *SAG*s from 68 species, including annual herbaceous plants such as *Arabidopsis*, rice, maize or sorghum, as well as perennial woody plants such as poplar. To our knowledge, LSD 3.0 is the only available resource specialized in leaf senescence, providing a convenient way to study leaf senescence via com-

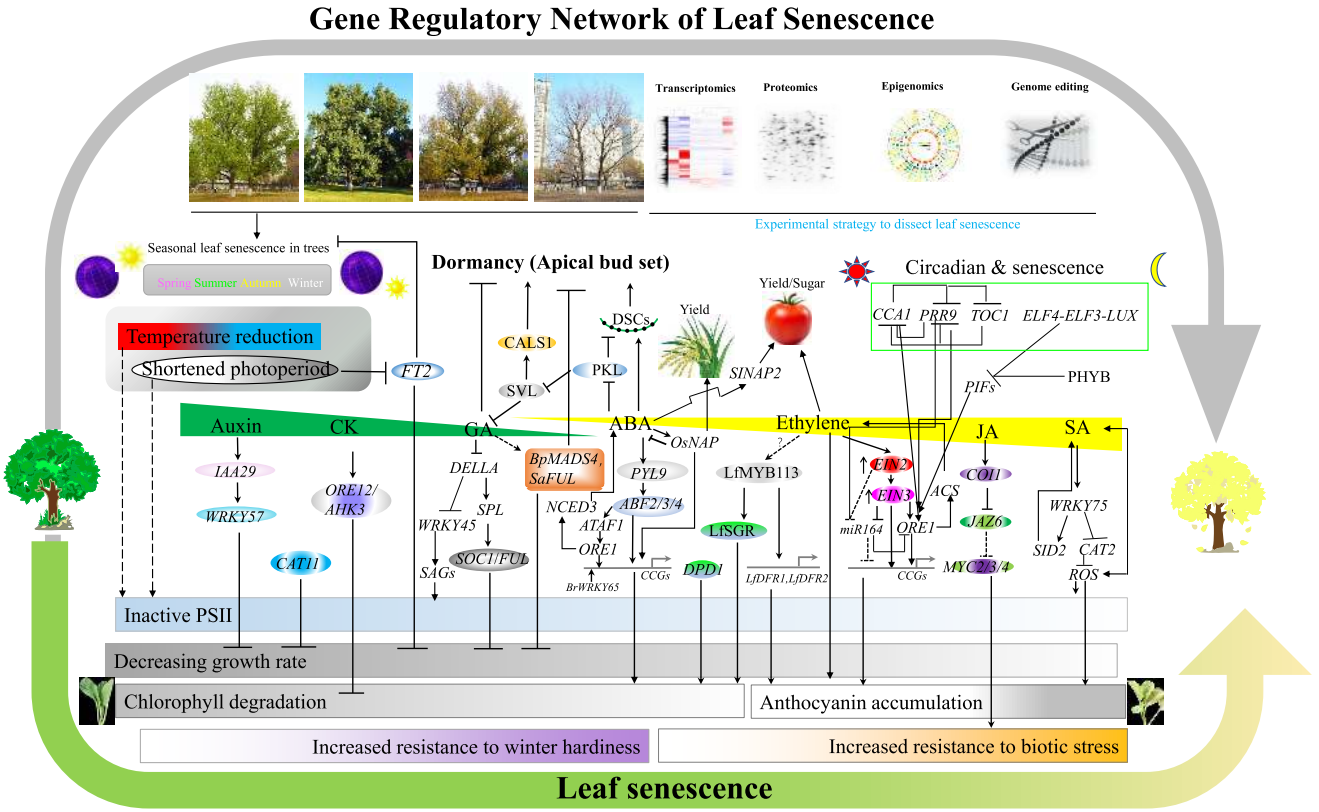

Figure 3. A gene regulatory network of leaf senescence with the integrated data from multiple species such as *Arabidopsis*, rice, rapeseed, tomato and poplar through an extensive literature survey.

parative biological strategy and construction of gene regulatory network (Figure 3). For example, the *Arabidopsis* NAC TF *AtNAP* has been demonstrated to be a key positive regulator of leaf senescence (30). Interestingly, a forward genetic screen shows that *OsNAP*, a homolog of *AtNAP*, also promotes leaf senQ`lescence in rice. More importantly, the silencing of *OsNAP* leads to an extension of the grain filling period and significantly increases grain yield (31). Because a lot of important breakthroughs for leaf senescence have been achieved in the model plant *Arabidopsis* (5), it is reasonable to translate these findings to guide senescence research in other plants. Toward this end, we listed the functional *SAG*s (delay or promote) as well as their curated annotations in *Arabidopsis* to help researchers identify the candidate *SAG*s in crops (Supplementary Tables S2 and 3), as testified by the fact that *SAG*s in maize, sorghum and cotton have been identified by using the LSD data (9,32,33). In addition, transcriptome data of leaf senescence in poplar deposited in LSD 3.0 could be helpful for us to perform a comparative analysis of leaf senescence between annual and perennial plants and explore the difference and/or similarity of their regulatory mechanisms.

To better serve the plant senescence research community, we plan to improve the database from the following aspects: (i) To integrate newly identified *SAG*s and mutant information via manual curation and computational annotation; (ii) To collect the senescence-associated phenotypes of ∼1150 ecotypes in the future because the ecotypes could help us better understand the relationship between senescence and environmental factors or other developmental traits such as flowering (Supplementary Figure S1); (iii) To collect worldwide publicly available publications (not limited to PubMed) related to leaf senescence; (iv) To update and improve web interfaces according to the suggestions from users; and (v) To develop online tools to facilitate comparative analysis of leaf senescence between annual and perennial plants. Taken together, considering that leaf senescence is a crucial biological process that exerts considerable influences on crop yield and quality, the updated LSD 3.0 would be of great help and broad utility for the plant research community.

SUPPLEMENTARY DATA

Supplementary Data are available at NAR Online.

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