# 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 (SAGs) 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 SensmRNAs 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 SAGs 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<sub>2</sub> 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 (SAGs) (5). Forward genetic studies of leaf senescence by screening senescencerelated mutants and reverse genetic analyses of SAGs 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 SAGs 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 SAGs. Currently,

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LSD has been widely used for functional studies of SAGs in *Arabidopsis* and systematic identification of SAGs 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 SAGs. 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 posttranscriptional 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 SAGs (13). The H3K27me3 demethylase REF6 positively regulates senescence process by directly upregulating SAGs, 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 RE-SISTANCE 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 SAGs (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 SAGs 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 SAGs 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, OTL, 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 SAGs. A typical example is *NOE1* (LOC\_Os03g03910) encoding a rice catalase. Loss-offunction of *NOE1* promotes leaf senescence by increasing the production of H<sub>2</sub>O<sub>2</sub> 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, proteinprotein 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	of gene n	umber among	the three	versions of LSD
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Species	LSD 1.0	LSD 2.0	LSD 3.0
Grain Amaranths (Amaranthus hypochondriacus)	0	1	1
Arabidopsis lyrata	0	2	2
Arabidopsis thaliana Chinese Milk Vetch (Astronalus sinicus)	1	3/44	3852
Birch (Betula pendula)	0	0	1
Cabbage (Brassica campestris)	0	2	2
Rapeseed (Brassica napus)	15	8	13
Broccoli (Brassica oleracea)	4	9	9
Chinese cabhage (Brassica rang subsp. Pekinensis)	0	1	1
Cabbage (Brassica rapa var. parachinensis)	0	5	19
Tea (Camellia sinensis)	0	1	3
Pepper ( <i>Capsicum annuum</i> )	0	1	3
Chrysenthemum (Chrysenthemum morifolium)	1	1	1
Sweet Orange ( <i>Citrus sinensis</i> )	0	0	4
Autumn Crocus ( <i>Crocus sativus</i> )	0	1	1
Muskmelon (Cucumis melo)	0	1	1
Carrot ( <i>Daucus carota</i> )	0	1	1
Carnation ( <i>Dianthus caryophyllus</i> ) Persimmon ( <i>Dianthus caryophyllus</i> )	0	1	1
Erianthus arundinaceus	0	0	1
Tall fescue (Festuca arundinacea)	0	1	1
Fescue (Festuca pratensis Huds)	1	1	1
Strawberry ( <i>Fragaria x ananassa</i> )	0	1	1
Soybean (Glycine max) Cotton (Gossynium hirsutum)	4	12	20
Sunflower ( <i>Helianthus annuus</i> )	0	0	5
Barley (Hordeum vulgare)	3	14	19
Sweet potato (Ipomoea batatas)	0	4	8
Japanese morning glory ( <i>Ipomoea nil</i> )	1	1	2
Easter lilv (Lilium longiflorum)	0	0	1
Litchi trees ( <i>Litchi chinensis</i> )	0	0	1
Perennial ryegrass (Lolium perenne)	0	4	5
Apple ( <i>Malus domestica</i> )	0	0	3
Chinese crabapple ( <i>Malus prunifolia</i> ) Mango ( <i>Mangifara indica</i> )	0	0	2
Alfalfa ( <i>Medicago sativa</i> )	1	2	3
Medicago truncatula	31	31	31
Miscanthus lutarioriparius	0	0	11
Mulberry (Morus alba)	0	0	1
Banana ( <i>Musa acuminata</i> ) Banana ( <i>Musa x paradisiaca</i> )	0	882	882
Bamboo ( <i>Neosinocalamus affinis</i> )	0	1	1
Coyote tobacco (Nicotiana attenuata)	0	1	1
Tobacco (Nicotiana tabacum)	5	9	18
Rice (Oryza sativa)	104	132	188
Picrorhiza (Picrorhiza kurrooa Rovle ex Benth)	0	0	1
Pea ( <i>Pisum sativum</i> )	4	6	6
Balloon flower (Platycodon grandiflorum)	0	1	1
Poplar (Populus tremula x Populus tremuloides)	0	0	198
Poplar (Populus trichocarpa) Peach (Prunus parsica I. Batsch)	0	0	1
Pear (Pvrus communis)	0	0	1
Radish ( <i>Raphanus sativus</i> )	0	0	1
Rose (Rosa hybrida)	1	1	1
Foxtail millet ( <i>Setaria italica</i> )	0	0 22	2
Potato (Solanum tycopersicon)	3	25	6
Sorghum (Sorghum bicolor)	4	26	26
Spinach (Spinacia oleracea)	0	2	2
Sugarcane	0	0	1
Wheat (Triticum aestivum) Wheat (Triticum turgidum)	1	256	259
Cowpea (Vigna unguiculata)	0	1	1
Maize (Zea mays)	3	94	98
Total 68	1145	5356	5853

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	Organism			Rice (Orvz	a sat	iva)				
ł	Taxonomic identi	fier		NCBI]		.,				
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	Ortholog Group Ortholog Groups Cross Link	Image: Signal System	E-value 5.7E-24	Accession miRNA Accession NP_00103 NP_00103 NP_00103 NP_00103 NP_00102 NP_56412 NP_56412 NP_56412 NP_56412 NP_00102 estExt_Ge est	5' A 3' G 3' G 1072 1073 1791 155 20 21 23 25673 88611 88635 15.1 15.1 88635 15.1 15.1 9.9w 9.9	GGGGAGA GT UUCUUU UUCUUU A A A A A A A A A A A A A	G :: ACCGUUCAUG UUGGUAAGUAU 2 0 0 3 1 0 3 1 0 3 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1	Taxon         Arabidopsis thaliana         Oryas sativa Japonica Group         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Physcomitrella patens subsp. patens         Ricinus communis         Ricinus communis         Volvox carten f		
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	Ortholog Group Ortholog Groups Ortholog Groups Database PIRSF PANTHER SUPERFAMILY ProSitePtofiles SMART Pram PRINTS ProSitePatterns	Image: Signal System           Entry ID           PIRSE038928           PTHR11465           SSF56634           PS51402           SM01060           PF00199           PR00067           PSD0067           PSD0067	E-value 5.7E-22 2.0E-22 75.1 1.9E-22 7.0E-14 2.1E-8 NA	Accession           NP_00103           NP_00103           NP_00103           NP_00103           NP_00103           NP_00103           NP_05412           NP_56412           NP_56412           NP_56412           NP_56412           NP_050106           egw1.33           estExt_Ge           estExt_Ge <td>5' A 3' G 3' G 1072 1073 1077 1077</td> <td>GGGGGAGA GL UUCUUU UUCUUU A A A A A A A A A A A A A</td> <td>G :: Cardinal Control Control</td> <td>3 ·         Taxon         Arabidopsis thaliana         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Physcomitrella patens subsp. patens         Ricinus communis         Ricinus communis         Ricinus communis         Ricinus communis         unctional, haem-containing, clades 1 and 3 uurctional, haem-containing         main         unctional, haem-containing         main         unctional, haem-co</td>	5' A 3' G 3' G 1072 1073 1077 1077	GGGGGAGA GL UUCUUU UUCUUU A A A A A A A A A A A A A	G :: Cardinal Control	3 ·         Taxon         Arabidopsis thaliana         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Physcomitrella patens subsp. patens         Ricinus communis         Ricinus communis         Ricinus communis         Ricinus communis         unctional, haem-containing, clades 1 and 3 uurctional, haem-containing         main         unctional, haem-containing         main         unctional, haem-co		
	Ortholog Group Ortholog Groups Ortholog Groups Definition of the second Definition of the second PiRSF PANTHER SUPERFAMILY ProSiteProfiles SMART ProSitePatterns PRINTS PRINTS DEINITS	Similar           : OG5_127182           : OG5_127182 <td :="" colspan="2" og5_127<="" td=""><td>E-valu 5.7E-22 7.0E-11 1.9E-22 7.0E-11 7.0E-12</td><td>Accession NP_00103 NP_00103 NP_00103 NP_00103 NP_00103 NP_00103 NP_00103 NP_00104 NP_00104 NP_00104 NP_00104 NP_00104 NP_00104 NP_00105 e_gwl.33 estExt_Ge fgenesh1 gw1.4424 2930.m0 30170.m0 XP_00295 Start 31 13 14 14 15 14 14 14 15 14</td><td>5' A 3' G 11072 11073 11073 11072 11073 11072 11073 11072 11073 11073 11072 11073 11074 11073 11074 11075 11075 11075 110</td><td>G GGGGAGA GL UUCUUUU UU A A C C C C C C C C C C C C C C C C C</td><td>G :: ACCGUUCAUG UUGGUAAGUAU 2 003910 ) 03910 ) 03910 ) 03910 ) 03910 ) 044 9 044 9 044 9 044 9 044 9 044 9 044 9 044 0 044 9 044 0 044 0 044 0 044 0 0 0 0 0 0 0 0 0 0 0 0 0</td><td>3 ·         Taxon         Arabidopsis thaliana         Chamydomonas reinhardtii         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Physcomitrella patens subsp. patens         Ricinus communis         Ricinus communis         Volvox carteri f. nagariensis         unctional, haem-containing         main         unctional, haem-containing         main         unctional, haem-containing         uredinal, haem-contatining</td></td>	<td>E-valu 5.7E-22 7.0E-11 1.9E-22 7.0E-11 7.0E-12</td> <td>Accession NP_00103 NP_00103 NP_00103 NP_00103 NP_00103 NP_00103 NP_00103 NP_00104 NP_00104 NP_00104 NP_00104 NP_00104 NP_00104 NP_00105 e_gwl.33 estExt_Ge fgenesh1 gw1.4424 2930.m0 30170.m0 XP_00295 Start 31 13 14 14 15 14 14 14 15 14</td> <td>5' A 3' G 11072 11073 11073 11072 11073 11072 11073 11072 11073 11073 11072 11073 11074 11073 11074 11075 11075 11075 110</td> <td>G GGGGAGA GL UUCUUUU UU A A C C C C C C C C C C C C C C C C C</td> <td>G :: ACCGUUCAUG UUGGUAAGUAU 2 003910 ) 03910 ) 03910 ) 03910 ) 03910 ) 044 9 044 9 044 9 044 9 044 9 044 9 044 9 044 0 044 9 044 0 044 0 044 0 044 0 0 0 0 0 0 0 0 0 0 0 0 0</td> <td>3 ·         Taxon         Arabidopsis thaliana         Chamydomonas reinhardtii         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Physcomitrella patens subsp. patens         Ricinus communis         Ricinus communis         Volvox carteri f. nagariensis         unctional, haem-containing         main         unctional, haem-containing         main         unctional, haem-containing         uredinal, haem-contatining</td>		E-valu 5.7E-22 7.0E-11 1.9E-22 7.0E-11 7.0E-12	Accession NP_00103 NP_00103 NP_00103 NP_00103 NP_00103 NP_00103 NP_00103 NP_00104 NP_00104 NP_00104 NP_00104 NP_00104 NP_00104 NP_00105 e_gwl.33 estExt_Ge fgenesh1 gw1.4424 2930.m0 30170.m0 XP_00295 Start 31 13 14 14 15 14 14 14 15 14	5' A 3' G 11072 11073 11073 11072 11073 11072 11073 11072 11073 11073 11072 11073 11074 11073 11074 11075 11075 11075 110	G GGGGAGA GL UUCUUUU UU A A C C C C C C C C C C C C C C C C C	G :: ACCGUUCAUG UUGGUAAGUAU 2 003910 ) 03910 ) 03910 ) 03910 ) 03910 ) 044 9 044 9 044 9 044 9 044 9 044 9 044 9 044 0 044 9 044 0 044 0 044 0 044 0 0 0 0 0 0 0 0 0 0 0 0 0	3 ·         Taxon         Arabidopsis thaliana         Chamydomonas reinhardtii         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Oryza sativa Japonica Group         Physcomitrella patens subsp. patens         Ricinus communis         Ricinus communis         Volvox carteri f. nagariensis         unctional, haem-containing         main         unctional, haem-containing         main         unctional, haem-containing         uredinal, haem-contatining
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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 *SAGs* in poplar. (A) Identification of *SAGs* by high-resolution temporal transcriptome of autumn leaf senescence in poplar. (B) Heat map showing the expression pattern of several *Sen-TFs* as leaves age in poplar. (C) Functional analysis of poplar *Sen-TFs* 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 fieldgrown poplar by RNA sequencing (Figure 2). In total, 678 SAGs 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-TFs) in poplar were identified and functionally characterized (Figure 2B). As shown in Figure 2C, overexpression of three poplar Sen-TFs (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-



# Gene Regulatory Network of Leaf Senescence

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 SAGs (delay or promote) as well as their curated annotations in Arabidopsis to help researchers identify the candidate SAGs in crops (Supplementary Tables S2 and 3), as testified by the fact that SAGs 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 SAGs 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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## REFERENCES

- 1. Zhu,X.G., Long,S.P. and Ort,D.R. (2010) Improving photosynthetic efficiency for greater yield. *Annu. Rev. Plant Biol.*, **61**, 235–261.
- Lim, P.O., Kim, H.J. and Nam, H.G. (2007) Leaf senescence. Annu. Rev. Plant Biol., 58, 115–136.
- 3. Guo, Y. and Gan, S. (2005) Leaf senescence: signals, execution, and regulation. *Cur.r Top. Dev. Biol.*, **71**, 83–112.
- Avila-Ospina, L., Moison, M., Yoshimoto, K. and Masclaux-Daubresse, C. (2014) Autophagy, plant senescence, and nutrient recycling. J. Exp. Bot., 65, 3799–3811.
- Kim, J., Woo, H.R. and Nam, H.G. (2016) Toward systems understanding of leaf senescence: an integrated multi-omics perspective on leaf senescence research. *Mol. Plant*, 9, 813–825.
- Woo,H.R., Kim,H.J., Lim,P.O. and Nam,H.G. (2019) Leaf senescence: systems and Dynamics aspects. *Annu. Rev. Plant Biol.*, 70, 347–376.
- Li,Z., Zhao,Y., Liu,X., Peng,J., Guo,H. and Luo,J. (2014) LSD 2.0: an update of the leaf senescence database. *Nucleic Acids Res.*, 42, D1200–D1205.
- Liu,X., Li,Z., Jiang,Z., Zhao,Y., Peng,J., Jin,J., Guo,H. and Luo,J. (2011) LSD: a leaf senescence database. *Nucleic Acids Res.*, 39, D1103–D1107.
- Wu,X.Y., Hu,W.J., Luo,H., Xia,Y., Zhao,Y., Wang,L.D., Zhang,L.M., Luo,J.C. and Jing,H.C. (2016) Transcriptome profiling of developmental leaf senescence in sorghum (*Sorghum bicolor*). *Plant Mol. Biol.*, 92, 555–580.
- Yang, J., Worley, E., Ma, Q., Li, J., Torres-Jerez, I., Li, G., Zhao, P.X., Xu, Y., Tang, Y. and Udvardi, M. (2016) Nitrogen remobilization and conservation, and underlying senescence-associated gene expression in the perennial switchgrass *Panicum virgatum*. *New Phytol.*, 211, 75–89.
- Guo, P., Li, Z., Huang, P., Li, B., Fang, S., Chu, J. and Guo, H. (2017) A tripartite amplification loop involving the transcription factor WRKY75, salicylic acid, and reactive oxygen species accelerates leaf senescence. *Plant Cell*, 29, 2854–2870.
- 12. Grosskinsky, D.K., Syaifullah, S.J. and Roitsch, T. (2018) Integration of multi-omics techniques and physiological phenotyping within a holistic phenomics approach to study senescence in model and crop plants. *J. Exp. Bot.*, **69**, 825–844.
- Liu,P., Zhang,S., Zhou,B., Luo,X., Zhou,X.F., Cai,B., Jin,Y.H., Niu, Lin,J., Cao,X. et al. (2019) The histone H3K4 demethylase JMJ16 represses leaf senescence in Arabidopsis. Plant Cell, 31, 430–443.
- Kim, H., Kim, H.J., Vu, Q.T., Jung, S., McClung, C.R., Hong, S. and Nam, H.G. (2018) Circadian control of ORE1 by PRR9 positively regulates leaf senescence in *Arabidopsis. Proc. Natl. Acad. Sci. U.S.A*, 115, 8448–8453.
- 15. Wang,Y., Zhang,Y. and Wang,L. (2018) Cross regulatory network between circadian clock and leaf senescence is emerging in higher plants. *Front. Plant Sci.*, **9**, 700.
- Kim,J.H., Woo,H.R., Kim,J., Lim,P.O., Lee,I.C., Choi,S.H., Hwang,D. and Nam,H.G. (2009) Trifurcate feed-forward regulation

of age-dependent cell death involving *miR164* in *Arabidopsis. Science*, **323**, 1053–1057.

- Li,Z., Peng,J., Wen,X. and Guo,H. (2013) Ethylene-insensitive3 is a senescence-associated gene that accelerates age-dependent leaf senescence by directly repressing *miR164* transcription in *Arabidopsis*. *Plant Cell*, 25, 3311–3328.
- Ay, N., Irmler, K., Fischer, A., Uhlemann, R., Reuter, G. and Humbeck, K. (2009) Epigenetic programming via histone methylation at WRKY53 controls leaf senescence in *Arabidopsis thaliana*. *Plant J.*, 58, 333–346.
- Wang,X., Gao,J., Gao,S., Song,Y., Yang,Z. and Kuai,B. (2019) The H3K27me3 demethylase REF6 promotes leaf senescence through directly activating major senescence regulatory and functional genes in *Arabidopsis. PLoS Genet.*, **15**, e1008068.
- Mao, C., Lu, S., Lv, B., Zhang, B., Shen, J., He, J., Luo, L., Xi, D., Chen, X. and Ming, F. (2017) A rice NAC transcription factor promotes leaf senescence via ABA biosynthesis. *Plant Physiol.*, **174**, 1747–1763.
- Li,Z., Woo,H.R. and Guo,H. (2018) Genetic redundancy of senescence-associated transcription factors in *Arabidopsis. J. Exp. Bot.*, 69, 811–823.
- Zhao, Y., Chan, Z., Gao, J., Xing, L., Cao, M., Yu, C., Hu, Y., You, J., Shi, H., Zhu, Y. *et al.* (2016) ABA receptor PYL9 promotes drought resistance and leaf senescence. *Proc. Natl. Acad. Sci. U.S.A.*, **113**, 1949–1954.
- Breeze, E., Harrison, E., McHattie, S., Hughes, L., Hickman, R., Hill, C., Kiddle, S., Kim, Y.S., Penfold, C.A., Jenkins, D. *et al.* (2011) High-resolution temporal profiling of transcripts during *Arabidopsis* leaf senescence reveals a distinct chronology of processes and regulation. *Plant Cell*, 23, 873–894.
- 24. Woo,H.R., Koo,H.J., Kim,J., Jeong,H., Yang,J.O., Lee,I.H., Jun,J.H., Choi,S.H., Park,S.J., Kang,B. *et al.* (2016) Programming of plant leaf senescence with temporal and inter-organellar coordination of transcriptome in *Arabidopsis. Plant Physiol.*, **171**, 452–467.
- BIG Data Center Members. (2019) Database Resources of the BIG Data Center in 2019. Nucleic Acids Res., 47, D8–D14.
- 26. Lin,A., Wang,Y., Tang,J., Xue,P., Li,C., Liu,L., Hu,B., Yang,F., Loake,G.J. and Chu,C. (2012) Nitric oxide and protein S-nitrosylation are integral to hydrogen peroxide-induced leaf cell death in rice. *Plant Physiol.*, **158**, 451–464.
- Tuskan,G.A., Difazio,S., Jansson,S., Bohlmann,J., Grigoriev,I., Hellsten,U., Putnam,N., Ralph,S., Rombauts,S., Salamov,A. *et al.* (2006) The genome of black cottonwood, *Populus trichocarpa (Torr. & Gray). Science*, **313**, 1596–1604.
- He, L., Wu, W., Zinta, G., Yang, L., Wang, D., Liu, R., Zhang, H., Zheng, Z., Huang, H., Zhang, Q. et al. (2018) A naturally occurring epiallele associates with leaf senescence and local climate adaptation in *Arabidopsis* accessions. *Nat. Commun.*, 9, 460.
- Lyu, J.I., Kim, J.H., Chu, H., Taylor, M.A., Jung, S., Baek, S.H., Woo, H.R., Lim, P.O. and Kim, J. (2019) Natural allelic variation of GVS1 confers diversity in the regulation of leaf senescence in *Arabidopsis. New Phytol.*, 221, 2320–2334.
- 30. Guo, Y. and Gan, S. (2006) AtNAP, a NAC family transcription factor, has an important role in leaf senescence. *Plant J.*, **46**, 601–612.
- 31. Liang, C., Wang, Y., Zhu, Y., Tang, J., Hu, B., Liu, L., Ou, S., Wu, H., Sun, X., Chu, J. *et al.* (2014) OsNAP connects abscisic acid and leaf senescence by fine-tuning abscisic acid biosynthesis and directly targeting senescence-associated genes in rice. *Proc. Natl. Acad. Sci.* U.S. A, 111, 10013–10018.
- 32. Lin, M., Lai, D., Pang, C., Fan, S., Song, M. and Yu, S. (2013) Generation and analysis of a large-scale expressed sequence Tag database from a full-length enriched cDNA library of developing leaves of *Gossypium hirsutum L. PLoS One*, **8**, e76443.
- 33. Sekhon, R.S., Šaski, C., Kumar, R., Flinn, B., Luo, F., Beissinger, T.M., Ackerman, A.J., Breitzman, M.W., Bridges, W.C., de Leon, N. *et al.* (2019) Integrated genome-scale analysis identifies novel genes and networks underlying senescence in maize. *Plant Cell*, **31**, 1968–1989.