

INVITED SPECIAL ARTICLE

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PhenoForecaster: A software package for the prediction of flowering phenology

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PREMISE OF THE STUDY: Predicting the flowering times of angiosperm taxa is a goal of mounting importance in the face of future climate change, with applications not only in plant biology and ecology, but also horticulture, agriculture, and invasive species management. To date, no tool is available to facilitate predictions of flowering phenology using multivariate phenoclimatic models. Such a tool is needed by researchers and other stakeholders who need to predict phenological activity, but are unfamiliar with phenoclimate modeling techniques. PhenoForecaster allows users of any background to conduct species-specific phenological predictions using an intuitive graphical interface and provides an estimate of each prediction's accuracy.

METHODS AND RESULTS: Elastic net regression techniques were used to develop species-specific models capable of predicting the flowering dates of 2320 angiosperm species.

CONCLUSIONS: PhenoForecaster is the first stand-alone package to make phenological modeling directly accessible to users without the need for in-depth phenological observations.

KEY WORDS bloom timing; elastic net regularization; flowering; herbarium specimens; phenoclimate models; phenological models; phenology.

Predicting the flowering time of angiosperm taxa under projected climate conditions or in locations at which flowering has not been observed is essential to the prediction of a wide array of ecological processes, including risk of frost damage to floral tissues (Cannell and Smith, 1986; Inouye, 2008), nectar and pollen availability to pollinators (Aldridge et al., 2011), and the intensity of competition for pollinators among co-flowering taxa (Waser, 1978; Rathcke, 1988a, b; Feldman et al., 2004). Phenological prediction can also be important to local tourism, and for determining the optimum time for herbicide or pesticide treatment. For example, accurate predictions of flowering time can prevent the planned application of pesticides during flowering, when beneficial insects and birds are visiting flowers. Similarly, the planned use of herbicides to suppress invasive plant species should occur before or during flowering, so as to minimize seed production. Consequently, the ability to predict the flowering times of angiosperm species is relevant not

only to ecologists and other researchers, but also to land managers and other professionals across a wide array of disciplines. In recent years, some tools have emerged to predict phenological timing under various climate conditions, such as the phenological forecast maps produced by Phenology Forecasts (<https://phenology.naturecast.org/>) or univariate phenological models produced by the USA National Phenology Network (<https://www.usanpn.org/data/visualizations>). To date, however, species-specific phenological models have been developed for only a small number of species, and such models have often required daily growing degree-day or chilling degree-day information, which until recently have not been readily available across the vast majority of locations, and have required significant technical expertise to utilize effectively. Furthermore, the output of such models is rarely bundled in such a way as to facilitate phenological predictions in the absence of extensive calculations or data manipulations on the part of the user.

In this paper, we present PhenoForecaster, a software package that allows users to predict quickly and easily the mean flowering date for each of 2320 angiosperm species. PhenoForecaster uses readily accessible climate data in combination with species-specific phenological models that were generated by the authors using a simplified version of a method previously used to evaluate phenological responses to climate using digital herbarium records (Park and Mazer, 2018). Specifically, PhenoForecaster uses estimates of five climate parameters (i.e., the quantity of winter and spring precipitation that fell as snow in a given year [PAS_wt and PAS_sp, respectively], the number of frost-free days that occurred in a given winter and spring [NFFD_wt and NFFD_sp, respectively], and the date of the beginning of the frost-free period [BFFP expressed as the Day of Year]) to predict the day of year (DOY) on which the selected angiosperm species will reach its mean flowering date (MFD) at a location experiencing those conditions. These parameters represent the climate cues to which MFD was found to be most sensitive across the majority of these species using similar data and modeling techniques to those used by PhenoForecaster (Park and Mazer, 2018). In order to facilitate PhenoForecaster's use, all of the phenoclimate models that it uses were limited to these climate parameters, which were sufficient to retain the majority of the predictive power produced by more complicated models (Park and Mazer, 2018). This package allows both manual entry of climate parameters as well as bulk entry of data in cases where phenological predictions are required across multiple locations or climate scenarios. PhenoForecaster has been designed to accept climate input in a comma-separated value (CSV) format that is compatible with climate data generated by ClimateNA (Wang et al., 2016), a freely available software package that produces spatially explicit estimates of historical climate conditions throughout North America, and which utilizes a user-friendly graphical interface and requires only that the user provide the latitude and longitude (either manually or as a CSV file) of all points of interest.

Thus, while predictions of phenological timing for a given plant species previously required extensive observation, modeling, and calculation, PhenoForecaster represents a simple-to-use tool through which the phenology of many angiosperm species can be readily predicted under any observed or theoretical climate scenario.

METHODS AND RESULTS

PhenoForecaster is an open source program written in Python 2.7 (Python Core Team, 2008). The source code, as well as the code used to construct the phenoclimate models used by PhenoForecaster, are available at <https://github.com/isaacWpark/PhenoForecaster>. A Windows installer package and source code, as well as a user's manual, are also available at <https://labs.eemb.ucsb.edu/mazer/susan/software>. To install the package, the user simply needs to download and run the installer. The executable has been successfully tested on Windows 7, 8, and 10. PhenoForecaster has an intuitive graphical user interface that allows users with minimal prior experience with phenological prediction or with PhenoForecaster to predict the phenological timing of any targeted species by implementing the following steps.

First, the user must select the subset of species-specific models from which they wish to choose, based on the minimum model reliability they desire. By default, only the 490 species-specific models

for which expected mean absolute error (MAE) ≤ 15 days (indicating that phenological predictions are, on average, typically within 15 days of observed MFDs) were considered to be "good" model fits, and are therefore displayed for selection. Depending on user preference, however, this list of species may be expanded to include species-specific models that exhibit higher MAE, or contracted to only display those species for which more accurate phenological models are available (Fig. 1A). Having filtered the species by the minimum MAE desired, the user must then use the species selection dropdown menu to select the species for which phenological predictions are to be generated (Fig. 1B). Second, the specific climatic conditions for which phenological predictions are desired may then be entered manually (Fig. 1C) or uploaded as a CSV data file (Fig. 1D). For the latter, the first line of the input file is a header line with column descriptions. The first two columns of the file, labeled 'ID1' and 'ID2', represent any string data the user desires to include for the purpose of identifying each row of data in a unique fashion. The remaining columns may be in any order, but must include the following: 'NFFD_wt', 'NFFD_sp', 'PAS_wt', 'PAS_sp', and 'BFFP'. Data in the column 'NFFD_wt' should consist of a count of the number of frost-free days from January 1 to March 31 in the year for which flowering time is to be estimated. Data in the column 'NFFD_sp' should consist of a count of the number of frost-free days from April 1 to June 30 in the year for which flowering time is to be estimated. Data in the column 'PAS_wt' should consist of the total precipitation that fell as snow (in mm) from January 1 to March 31 in the year for which flowering time is to be estimated. Data in the column 'PAS_sp' should consist of the total precipitation that fell as snow (in mm) from April 1 to June 30 in the year for which flowering time is to be estimated. Data in the column 'BFFP' should consist of the DOY on which the annual frost-free period began. PhenoForecaster allows any number of additional data columns (representing other data that may be associated with each location or year to be predicted) to be placed into the input file. In cases where the user desires that data from such additional columns be preserved in the output file created by PhenoForecaster, they may select the 'retain all input data' option in the lower left of the user interface. If this option is selected, PhenoForecaster will preserve all columns from the input data, appending a new column with the header 'DOY_Predicted' that consists of the predicted MFD for a given row of data, and output all data as a CSV file. Otherwise, PhenoForecaster will generate output in the form of a CSV file, with the headers 'ID1', 'ID2', and 'DOY_Predicted.'

PhenoForecaster utilizes phenoclimate models that were constructed for each species from herbarium-based phenological data using a total of 556,322 digital records of herbarium specimens collected in flower across 72 herbaria throughout North America (see Acknowledgments for complete listing), collected between 1901 and 2015 and structured in Darwin Core format. Specimens that did not include either the decimal latitude and longitude from which the sample was collected or the precise date of collection were eliminated. Specimens that were not explicitly recorded as being in flower within either the Darwin Core fields 'reproductive-condition' or 'lifestage' were eliminated. Specimens that were only listed as 'in bud' or 'fruiting' were not considered to be in flower for purposes of this analysis. Duplicate specimens (i.e., specimens of a given species that were collected on the same date and from the same location) were also excluded from analysis. Each remaining specimen therefore represented a single phenological observation. Phenological models derived using herbarium-based observations

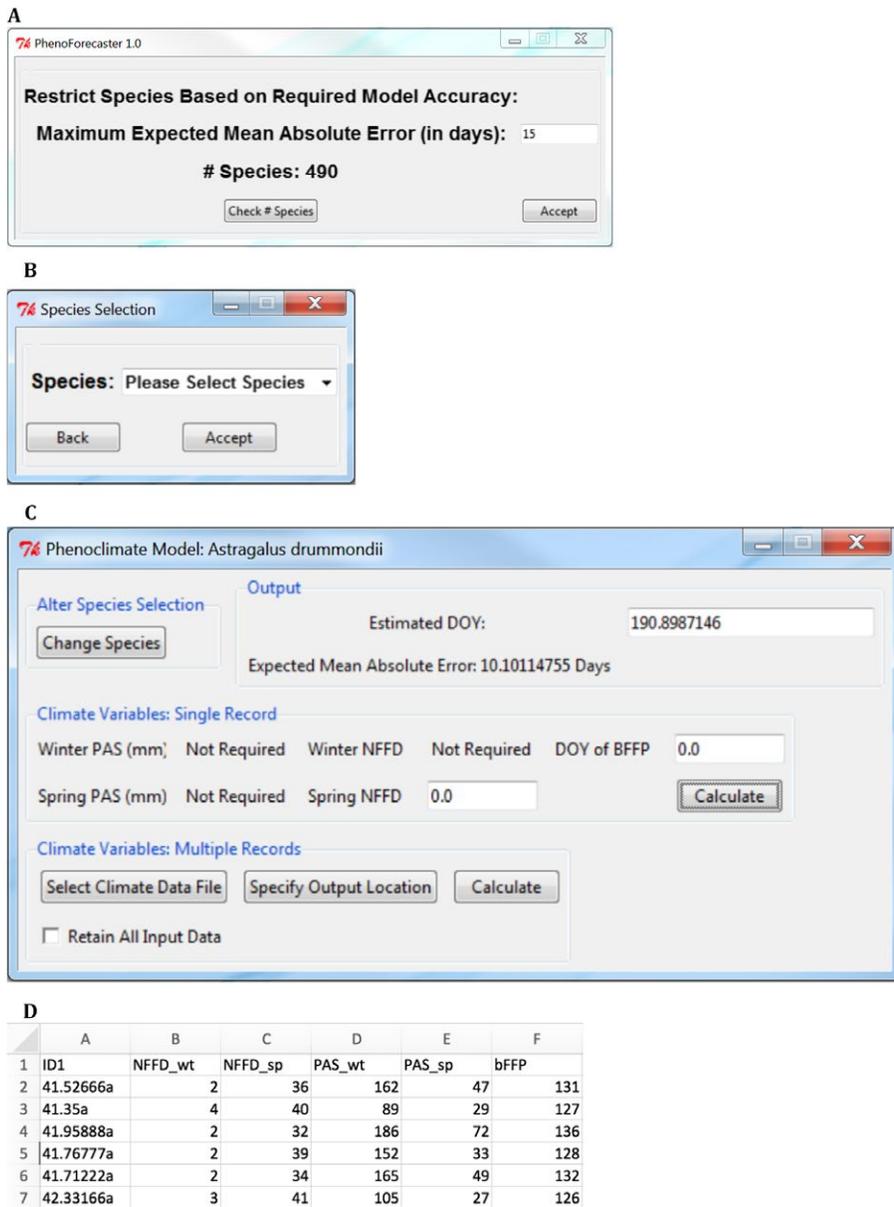


FIGURE 1. User interface for PhenoForecaster. (A) First, the list of available species is restricted to those species for which expected mean absolute error (MAE) in days is equal or less than the desired accuracy. (B) The target species is selected using the species selection dropdown. (C) Climate conditions (i.e., the seasonal quantity of precipitation as snow [PAS], the seasonal number of frost-free days [NFFD], and the date on which the annual frost-free period began [BFFP]) may then either be entered manually using the Single Record menu, or in bulk by selecting the relevant data files and output locations using the Multiple Records menu. (D) Example input data file. Additional columns may be added as desired.

of flowering phenology have been found to accurately predict shifts in phenological events that were observed in situ in response to climate changes (Primack et al., 2004; Miller-Rushing et al., 2006; Park and Mazer, 2018).

Species-specific models of MFD for each species were conducted using elastic net regularization, which has previously been demonstrated to be an effective method for predicting the flowering times of angiosperm taxa using herbarium specimens (Park and Mazer, 2018). For the models used by PhenoForecaster, winter and spring

climate conditions (consisting of NFFD, PAS, and BFFP) at the location and DOY from which each specimen was collected were first estimated using the software package ClimateNA (Wang et al., 2016). Each species-specific phenoclimatic model was then constructed using elastic net regularization, a multivariate regression method that, rather than selecting or removing parameters in a binary fashion as with forward or backward selection, enforces parsimony by penalizing model complexity using two penalty terms: the sum of the absolute value of all parameter coefficients (L1, Eq. 1a), and the sum of all parameter coefficients squared (L2, Eq. 1b [Zou and Hastie, 2005; De Mol et al., 2009]).

$$L1 = \sum \|\beta\| \quad (1a)$$

$$L2 = \sum \|\beta^2\| \quad (1b)$$

A penalty weighting term (α) controls the degree to which model complexity is penalized. Similarly, the relative penalization of L1 versus L2 is controlled by a relative weighting term (ρ). The model for which the sum of the SSE (sum of squared errors) and the L1 and L2 penalties, modified by the two weighting terms, is minimized (C; Eq. 2) is selected as the optimal model.

$$C = SSE + \alpha\rho\|L1\| + \alpha(1 - \rho)\|L2\| \quad (2)$$

This method has substantial advantages over stepwise forward selection or backward elimination regression techniques, particularly when handling data sets in which multiple explanatory factors are likely to exhibit some degree of collinearity, such as is common in climatic data (Rawal et al., 2015). Elastic net regression has been found to generate models that remain highly stable in cases where multiple explanatory factors exhibit collinearity (Zou and Hastie, 2005), while avoiding the variance inflation that often occurs when using stepwise regression techniques (De Mol et al., 2009; Raschkla and Mirjalili, 2017).

For each angiosperm species that was represented by 100 or more specimens in our herbarium-based data set, phenological models were constructed to predict the MFD of that species from local climate conditions using the elasticCV class contained within Scikit-Learn 0.814-4 in Python, which conducts an internally cross-validated version of elastic net regularization that selects the optimal values for the weighting terms ρ and α in order to minimize both model complexity and standard error (Appendix S1).

The models used for each species in this study were constructed through iterative fitting along a regularization path,

using 100 values of α and 22 values of ρ (ranging from 0.01 to 0.99). The optimal model coefficients were then selected using 25-fold cross-validation. The MAE for each model represents the mean MAE of the 25 iterations in which it was trained and tested using separate data sets; this value therefore represents the expected degree of error (in days) that may be expected for phenological predictions of a given species under novel conditions (Fig. 2). Additionally, the accuracy of these species-specific models was tested for three species using observations of mean flowering time derived from in situ phenological observations provided by the USA National Phenology Network database. The models used by PhenoForecaster predicted the timing of both in situ and herbarium-based observations of mean flowering with similar accuracy (as measured by MAE, Appendix S2). Species for which phenoclimate models produced MAE values of <15 days were considered to exhibit “good” model fits (and therefore available for selection in PhenoForecaster) by default. However, PhenoForecaster allows users to alter the MAE threshold that they consider to represent “good” model performance to accommodate cases where higher or lower predictive accuracy is required. For 186 of the 2320 species examined here, the cross-validated MAE produced by the phenological model was identical to that estimated using the collection dates of the specimens alone (i.e., without selecting climate parameters). Although these species were retained for use in PhenoForecaster, it should be noted that no climate data may be entered for these species, and the resulting predictions of flowering time consist only of a constant value reflecting an estimate of the mean observed flowering date for that species, which is not influenced by local climate conditions. Additional species will be added and models will be updated as new data or superior modeling techniques become available. Updated versions of this program will be hosted at <https://labs.eemb.ucsb.edu/mazer/susan/software>.

CONCLUSIONS

Although many studies have examined patterns of phenological variation in response to local climate, few tools exist for the

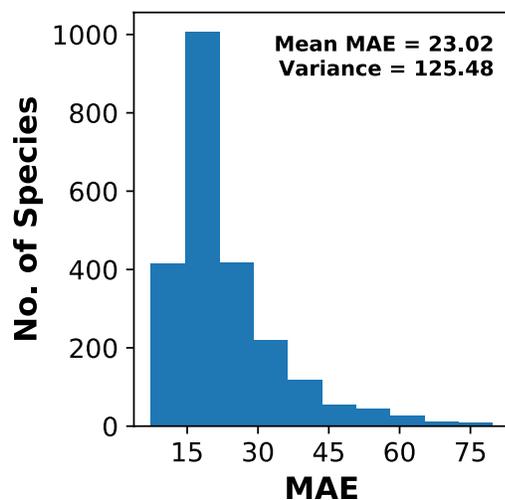


FIGURE 2. Distribution of mean absolute error (MAE) among species.

prediction of phenological timing under novel climate conditions. PhenoForecaster provides a free, quick, and easy-to-use software package that allows researchers of any background to quickly predict the mean flowering date of angiosperm species under novel annual conditions, or at locations where the phenology of that species has not previously been observed. Its intuitive user interface and compatibility with existing spatial climate estimation packages such as ClimateNA (Wang et al., 2016) make phenological prediction easy to accomplish by researchers of any background without the need for extensive training or familiarity with phenoclimate modeling. It should be noted, however, that the accuracy of predictions by PhenoForecaster is variable and depends highly on the species selected for prediction. The expected accuracy of PhenoForecaster output, as reflected by the MAE value for that species, should be kept in mind when dealing with predicted MFD values generated by PhenoForecaster. Furthermore, these models do not account for potential heterogeneity of phenological responsiveness among populations of a given species, but instead represent mean phenological responsiveness across all available specimens for each species. These data were also based on models trained using phenological observations throughout North America only, and using derived estimates of local climate condition produced using ClimateNA; these estimates may exhibit some differences from ground-based observations of these climate parameters, or from estimates of these climate parameters derived using different methods. Thus, predictions of the phenology of these species outside of North America, or based on different sources of climate data, should be treated with caution. In addition, it should be remembered that PhenoForecaster models the timing of MFD only, and that the relationship of MFD to other phenophases, such as leaf-out, date of first flower, or date of last flower, may be highly variable among species and across climate gradients. These predictions should therefore be treated as dates on which the individuals of a given species are likely to be in flower where they have experienced a particular suite of climatic conditions, rather than as the onset or termination date of any specific phenophase. Where possible, we also recommend cross-checking predicted MFD values generated by PhenoForecaster against observed MFD values for that species, particularly when evaluating the phenology of a species under conditions that are outside of its historical range limits. Nevertheless, PhenoForecaster represents a freely available and powerful tool that allows any researcher to conduct rapid predictions of phenological timing under past, projected, or otherwise novel climate conditions.

ACKNOWLEDGMENTS

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DATA ACCESSIBILITY

The PhenoForecaster source code, as well as the code used to construct the phenoclimate models, are available at <https://github.com/isaacWpark/PhenoForecaster>. A Windows installer package and source code, as well as a user's manual, are available at <https://labs.eemb.ucsb.edu/mazer/susan/software>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Model parameters and predicted mean absolute error (MAE) for all species.

APPENDIX S2. Mean absolute error (MAE) of species-specific phenological model outputs in predicting (1) herbarium-based phenological observations not present in model training and (2) in situ phenological observations of mean flowering time (referred to as “in situ MAE”).

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APPENDIX 1. List of contributing herbaria.

Institution name	Herbarium name	Index Herbarium code
Yale University	Peabody Museum of Natural History Herbarium	YU
University of Connecticut	George Safford Torrey Herbarium	CONN
Acadia University	E. C. Smith Herbarium	CHRB
University of Montreal	Marie-Victorin Herbarium	MT
Harvard University	Harvard University Herbaria	A, AMES, ECON, FH, GH, NEBC
University of New Hampshire	Albion Hodgson Herbarium	NHA
Drexel University	The herbarium of the Academy of Natural Sciences of Drexel University	PH
University of California–Berkeley	Jepson Herbarium	JEPS
University of California–Berkeley	Sagehen Field Station Herbarium	SCFS
California Polytechnic State University	California Polytechnic State University Herbarium	OBI
University of Santa Cruz	University of Santa Cruz Herbarium	UCSC
Black Hills State University	Black Hills State University Herbarium	BHSC
Luther College	Luther College Herbarium	LCDI
Minot State University	Minot State University Herbarium	MISU
Tarleton State University	Tarleton State University Herbarium	TAC
South Dakota State University	C. A. Taylor Herbarium	SDSU-SDC
Pittsburg State University	Theodore M. Sperry Herbarium	KSP
Montana State University	Billings Herbarium	MSUB
Sul Ross University	A. Michael Powell Herbarium	SRSC
Fort Hays State University	Fort Hays State University Herbarium	FHKSC
Utah State University	Intermountain Herbarium	USU-UTC

(Continues)

APPENDIX 1 (continued)

Institution name	Herbarium name	Index Herbariorum code
Brigham Young University	S. L. Welsh Herbarium	BRY-V
Eastern Nevada Landscape Coalition	Eastern Nevada Landscape Coalition Herbarium	ENLC
University of Nevada	Reno Herbarium	RENO-V
Natural History Museum of Utah	Garrett Herbarium	UT-Botany
Western Illinois University	R. M. Myers Herbarium	MWI
Eastern Illinois University	Stover-Ebinger Herbarium	EIU
Northern Illinois University	Northern Illinois University Herbarium	DEK
Morton Arboretum	Morton Arboretum Herbarium	MOR
Chicago Botanic Garden	Chicago Botanic Garden Herbarium	CHIC
Field Museum of Natural History	Field Museum of Natural History	F-Botany
University of Wisconsin–Madison	University of Wisconsin–Madison, Wisconsin State Herbarium	WIS
University of Michigan	University of Michigan Herbarium	MICH
Indiana University	Deam Herbarium	IND
Universidad de Sonora	Universidad de Sonora Herbarium	USON
Centro de Investigaciones Biológicas del Noroeste, S.C.	Observaciones Generales de Flora del Noroeste de México	RHNM
Instituto Politécnico Nacional–Unidad Durango	Herbario del Instituto Politécnico Nacional–Unidad Durango	CIIDIR
University of California–Riverside	University of California–Riverside Herbarium	UCR
San Diego State University	San Diego State University Herbarium	SDSU
Granite Mountains Desert Research Center	Granite Mountains Desert Research Center	GMDRC
University of South Carolina	A. C. Moore Herbarium	USCH
Auburn University	John D. Freeman Herbarium	AUA
Clemson University	Clemson University Herbarium	CLEMS
Eastern Kentucky University	Ronald L. Jones Herbarium	EKY
College of William and Mary	College of William and Mary Herbarium	WILLI
Appalachian State University	I. W. Carpenter, Jr. Herbarium	BOON
University of North Carolina	University of North Carolina Chapel Hill Herbarium	NCU
University of Memphis	University of Memphis Herbarium	MEM
Mississippi State University	Mississippi State University Herbarium	MISSA
University of Mississippi	Thomas M. Pullen Herbarium	MISS
University of Southern Mississippi	University of Southern Mississippi Herbarium	USMS
Mississippi Museum of Natural Science	Mississippi Museum of Natural Science Herbarium	MMNS
Marshall University	Marshall University Herbarium	MUHW
Longwood University	Harvill-Stevens Herbarium	FARM
Western Carolina University	Western Carolina University Herbarium	WCUH
Northern Kentucky University	John W. Thieret Herbarium	KNK
Salem College	Salem College Herbarium	SC
Troy University	Troy University Herbarium	TROY
Arizona State University	Arizona State University Herbarium	ASU-Plants
University of Arizona	University of Arizona Herbarium	ARIZ
Desert Botanical Garden	Desert Botanical Garden Herbarium	DES
Northern Arizona University	Deaver Herbarium	ASC
Navajo Nation Department of Fish and Wildlife	Navajo Nation Herbarium	NAVA
Grand Canyon National Park	Grand Canyon National Park Herbarium	GKNP
University of New Mexico	University of New Mexico Herbarium	UNM-Vascular Plants
Western New Mexico University	Dale A. Zimmerman Herbarium	SNM
Museum of Northern Arizona	Museum of Northern Arizona Herbarium	MNA
Gila National Forest	Gila National Forest Herbarium	USFS-GILA
Arizona Western College	Arizona Western College Herbarium	AWC
Natural History Institute	Natural History Institute Herbarium	NHI