Cottonwood Seed Dispersal on the Trinity River
2018 Synthesis Report

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ABSTRACT

Severe degradation of habitat from historic mining and significant flow diversions for several decades on the Trinity River led to the near-collapse of the salmonid fisheries, which instigated recovery efforts that culminated in a 2000 Record of Decision to create the Trinity River Restoration Program (TRRP) and adopt the rehabilitation objectives and strategies outlined in the science-based *Trinity River Flow Evaluation Final Report* (TRFE). One specific riparian vegetation objective was to encourage riparian germination and establishment (especially of black cottonwood and tree willows) onto bar crests and floodplain surfaces in Normal and wetter water years. The TRFE presented qualitative seed dispersal periods for black cottonwood that served as a guide to annual flow release planning; however, after a decade of ROD flows, black cottonwood recruitment is not occurring to the extent expected, and the defined seed dispersal window is being re-evaluated. The goal of this report is to quantify the seed dispersal period that can be consistently applied during annual flow scheduling so that the timing of intentional flow benches (e.g., 169.9 cms) coincides with cottonwood seed release.

Seed dispersal occurred between April 19 and July 3 during five years of monitoring. Sometimes seed dispersal occurred earlier within this broad window (e.g., in 2004, 2015, 2016), and sometimes later (2017, 2018). Therefore, further analyses were conducted to refine the broad seed dispersal window into a target seed dispersal period for annual flow release planning. Survey weeks 10 and 11 had the highest median seed dispersal, and seed dispersal for all trees always occurred during these two weeks. Therefore, the calendar dates corresponding to survey weeks 10 and 11 (May 15 to May 28) are recommended as the black cottonwood target seed dispersal period for annual flow release planning. The target seed dispersal period corresponded well to actual ROD releases during the years when seed dispersal was monitored.

We examined two potential causal factors influencing the timing of seed dispersal: photoperiod and air temperature. These factors were chosen largely due to the availability of data. We used Julian date as a proxy for photoperiod and accumulated degree-hours as a proxy for air temperature. Seed dispersal did not occur before 2,000 accumulated degree-hours during 2015–2018 and was nearly always completed by 3,000 accumulated degree-hours.

We developed a predictive generalized linear model (GLM) for a binomial distribution to develop the best statistical relationships between seed dispersal (response variable) and selected predictor variables (Julian date, accumulated degree-hours) to predict the timing of the highest probability of seed dispersal occurring in any year. There is a 72% probability of seed dispersal on Julian date 139 (May 19), regardless of the accumulated degree-hour value on that date. May 19 is within the target seed dispersal period, which according to the model, will capture the highest probability of seed dispersal in hotter years and increasing (though not the highest) probabilities of seed dispersal in cooler years.

Seed dispersal monitoring should be continued to meet sample size requirements and improve management flexibility in response to climate change. The model developed here was used in WY 2019 annual flow planning and can continue to be used in future flow planning by targeting May 19 as the beginning of seed dispersal and scheduling flow ramp-downs to coincide with this date. A continuation of seed dispersal monitoring can facilitate any necessary changes to flow scheduling based on field observations, while also providing additional data to improve the model. A truly predictive model that reflects environmental variables that influence seed dispersal timing should be developed to allow annual flow release planning to incorporate annual conditions earlier in the planning process (i.e., warmer years might use a modified target seed dispersal period). Site-specific environmental conditions have not been monitored and therefore data are not available. Coupling future seed dispersal observations with local environmental monitoring (via HOBO sensors) could improve the predictive model and contribute to climate change monitoring and scientific knowledge.

1 INTRODUCTION

Black cottonwood (*Populus trichocarpa*) is an iconic foundation species common in riparian areas in the western United States. Black cottonwoods are fast-growing, can live upwards of 200 years, and provide important habitat benefits throughout their lifespan, including the ability to fix nitrogen (Roe 1958, Burns and Honkala 1990, Doty et al. 2016). Saplings and young trees provide food and cover for many mammal species, such as rabbits, deer, elk, and moose (Steinberg 2001). As mature trees, they create vegetative structure, forming the tallest layer of most riparian canopies. Cottonwoods provide essential habitat for migratory neotropical birds, especially riparian focal species (RHJV Bailey 1912, 2004, Nur et al. 2008). Black cottonwood provides shade to maintain low stream temperatures and contributes organic leaf matter important to stream nutrient cycling, and abundant nesting and roosting sites for a plethora of bird species (Nesom 2003). Cottonwoods are the preferred food and building material of American beavers (Henker 2009). Even as they senesce with age, cottonwoods provide extremely important habitat for cavity nesting birds (Sedgewick and Knopf 1990) and many species who take up residence in abandoned cavity nests. Dead trees may remain standing for decades, serving as host to fungi, insects, birds, bats, and other mammals. Fallen trees may contribute large wood to the stream channel immediately or may remain on the floodplain to provide instream fish habitat at higher streamflows.

The black cottonwood life history strategy is adapted to the annual cycle of springtime flooding, which is often the result of snowmelt (Noble 1979, Braatne et al. 1996). Changes in land use, including urbanization, flow diversion, and various mining activities, have greatly reduced the extent of black cottonwoods. Flow regulation especially has the potential to decouple black cottonwood seed dispersal from the historical flow regimes to which it has adapted (Rood and Mahoney 1990, Braatne et al. 1996, Braatne et al. 2007).

River regulation may negatively impact black cottonwood recruitment. Reservoirs in the western United States are often designed to capture spring runoff and redistribute the annual water yield during drier months to municipal and agricultural water use via canals. Water that is not diverted is released and is often the minimum amount of water needed to maintain fishery resources. Cottonwoods may geminate and attempt to colonize lower bank margins and gravel bars but are prone to flood scour and inundation mortality during winter months. If flow releases are not timed to coincide with the local cottonwood seed dispersal period, the necessary physical seedbeds and soil moisture may be either inundated or too dry to facilitate seedling establishment. Over the last two decades, streamflow restoration has targeted cottonwood recruitment (M&T 1997, Roberts et al. 2002, Rood et al. 2003, Stillwater Sciences et al. 2006). However, flows may be poorly timed to coincide with the cottonwood seed dispersal period and thus unable to capture the seed dispersal window or may be of insufficient magnitude to adequately prepare suitable nursery sites for germination and establishment (Tiedemann 2011).

Woody flowering plants that live for more than a few years follow annual life history patterns of dormancy, breaking bud and leafing out, flowering, seed dispersal, and leaf abscission. Seasonal and interannual variations in temperature, relative humidity, and competition may influence woody flowering plants' annual life history patterns. Black cottonwood is commonly known throughout its range to flower in early spring and begin dispersing seeds in late spring to early summer, with actual timing varying by latitude and elevation (Braatne et al. 1996). This generality is useful when considering the timing of broad seasonal changes (e.g., winter to spring), but it does not provide the specificity required when considering hydrograph timing on a regulated river to promote cottonwood seed germination and establishment. Seed dispersal itself lasts approximately 39 days (Stillwater Sciences et al. 2006), but if the timing of peak flows and rate of flow recession do not coincide with cottonwood seed dispersal, water released for the intended effect of cottonwood seedling initiation may not achieve riparian regeneration. Variation in phenological timing can be high within a single stand of the same species (Lechowicz 1984, Boes and Strauss 1994), even though the average timing of each stage is reliable from year to year (Farmer 1966). This is likely due to strong genetic control of phenological timing.

Some cottonwood trees may disperse seeds early while other may disperse seeds later within populations of the same species. In black cottonwood, early seeders release their seeds early in the seed dispersal period, when streamflows may be high and suitable sites are inundated or likely to be scoured. The advantage is that, during drier years, the early seeders will find the suitable nursery sites and be able to grow roots down with the earlier-than-usual receding groundwater (Scott et al. 1996). Late seeders, in contrast, release their seeds toward the end of the seed dispersal period. They rely on later high flows typical of wetter water years, when suitable sites are inundated for longer and thus unavailable to seeds released in the first part of the seed dispersal period (Scott et al. 1996). Both early seeders and late seeders represent genetic diversity within a population that has adapted to local conditions (Verdú and Traveset 2005). Successful seed germination and seedling establishment is episodic rather than annual and relies on the right combination of environmental factors. By maintaining a population that includes both early and late seeding individuals, the adaptation capacity of the population is improved.

Cottonwood flowering occurs in response to photoperiod (i.e., day length), vernalization (accumulated cold temperatures), degree-days (accumulated warm temperatures), and perhaps other factors, but the specific relationships between these variables and seed dispersal in cottonwoods is not well understood (Stella et al. 2006, Andrés and Coupland 2012, Rinne et al. 2018). Vernalization acts to suppress a plant's response to photoperiod until a certain temperature threshold is reached. (Kim et al. 2009). But flowers are highly susceptible to frost, and entire crops can be lost overnight (J. Mcsloy, pers. comm.). Low temperatures (vernalization) promote sexual reproduction in cottonwood (Andrés and Coupland 2012).

Cottonwood seed dispersal timing may vary annually depending on weather conditions (Stella et al. 2006, Cao et al. 2009, Herbison et al. 2015, Polzin and Rood 2017). Capsules dehisce and release their seeds as conditions become drier in semi-arid locations (Stella et al. 2006); in humid climates, summer rain events can trigger black cottonwood seed release from mature capsules (Herbison et al. 2015, Polzin and Rood 2017). Wind speed and relative humidity can affect the timing of seed dispersal in desert poplar (*P. euphratica,* Cao et al. 2009). Stronger, taller seedlings result from germination that occurs between 5 °C and 28.9 °C (41 °F and 84 °F, Schreiner 1974), which suggests that optimal seedling survival would result from seed dispersal that occurs in early spring as air temperatures warm, but before daily air temperatures become too hot.

2 BACKGROUND

The Trinity River, tributary to the Klamath River in northern California (Figure 1), has a residual population of black cottonwood that has survived climatic and extensive anthropogenic-induced changes. The Trinity River has been completely altered from its pre-European-settlement channel form (BLM 1995, USFWS and HVT 1999, Krause et al. 2010, AECOM 2013). Beginning around 1850 with the discovery of gold in the watershed, the Trinity River experienced extensive mining operations that lasted approximately 100 years (Figure 2). In addition to some of the largest hydraulic mines in California, the Trinity River valley was first placer mined, and then systematically dredged and turned over. Floodplains that had formed under the historic pre-diversion hydrology were completely eliminated. Early settlement records of the riparian corridor stand structure or species are unavailable to guide present day restoration efforts. Mining waned after World War II, and construction of two dams in the late 1950's and early 1960's as part of the Trinity River Division (TRD) of the Central Valley Improvement Project, led to significant flow diversions. The TRD captured snowmelt from the Trinity Alps and stored it in Trinity Lake, effectively eliminating the snowmelt portion of the hydrograph to the downstream river, to which many local species had co-evolved. The absence of variable streamflows characterized by spring snowmelt disrupted the life histories of several species, including black cottonwood and Chinook Salmon (*Oncorhynchus tshawytscha)*.

The near-collapse of the salmonid fisheries in the Trinity River instigated recovery efforts that culminated in the science-based *Trinity River Flow Evaluation Report* (TRFE; (TRFE; USFWS and HVT 1999), which outlined rehabilitation objectives and strategies to meet those objectives. The Secretary of the Interior adopted the recommendations in the TRFE in a 2000 Record of Decision (ROD). The Trinity River Restoration Program (TRRP) was created to implement the ROD, which has a goal to restore and sustain natural production of anadromous fish populations downstream of Lewiston Dam to pre-dam levels to facilitate dependent tribal, commercial, and sport fisheries' full participation in the benefits of restoration via enhanced harvest opportunities (TRRP and ESSA Technologies 2009). Actions specified by the TRFE and adopted in the ROD that are necessary to restore and maintain the freshwater habitats for anadromous salmonids to achieve this goal are: (1) mechanical rehabilitation of the channel, (2) flow management to restore fluvial processes that create and maintain suitable salmonid habitat and to meet water temperature objectives for juvenile and adult salmonids, (3) coarse and fine sediment management, and (4) watershed restoration (DOI 2000).

The TRFE identified specific riparian vegetation objectives for different geomorphic features and water year classes (USFWS and HVT 1999). Inhibiting riparian encroachment (especially of narrowleaf willows and white alders) onto active bars and channel margins was an objective in all water year classes, while encouraging riparian germination and establishment (especially of black cottonwood and tree willows) onto bar crests and floodplain surfaces was an objective in Normal and wetter years. The TRFE presented qualitative seed dispersal periods for black cottonwood that served as a guide to annual flow release planning (Bair 2001).

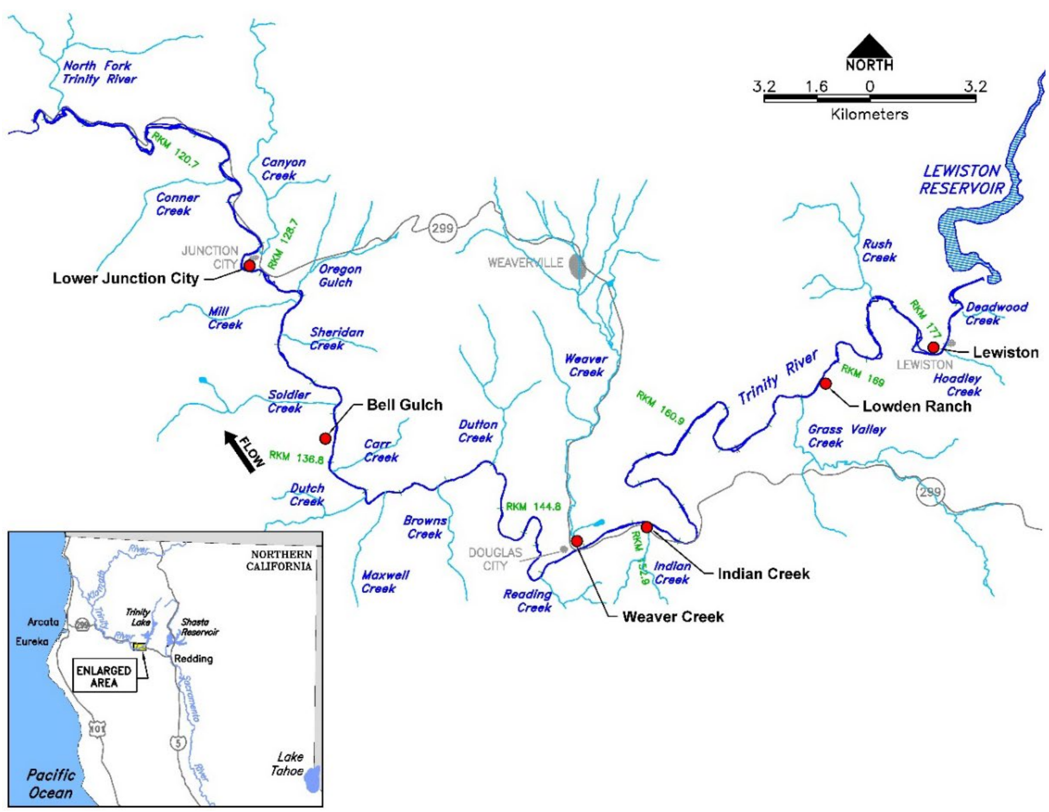

Figure 1. Trinity River location map, highlighting the 64-km Project Reach from Lewiston Dam to the North Fork Trinity River. Red dots indicate seed dispersal monitoring sites, green numbers indicate River Kilometer (RKm).

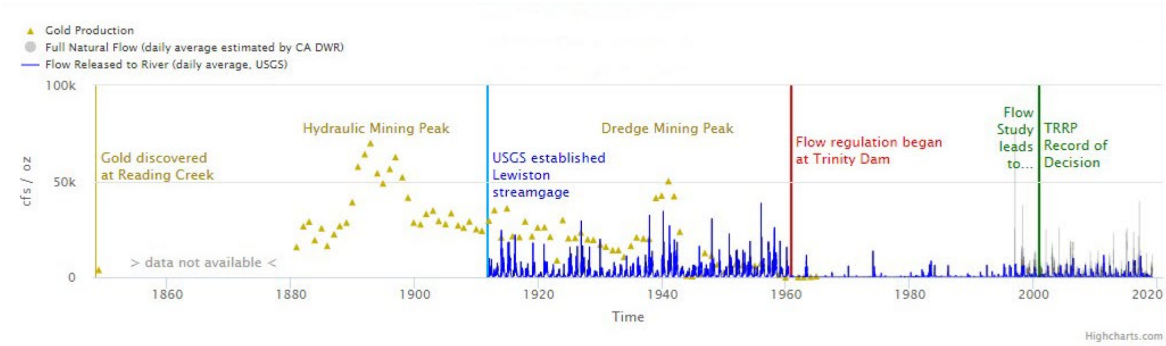

Figure 2. Timeline of human activity in the Project Reach of the Trinity River, California, from approximately 1850 to present. Figure adapted from TRRP (2018).

ROD releases from Lewiston Dam were expected to create a scaled-down (compared to pre-dam), dynamic, alluvial river with active bars, reconnected floodplains, and diverse and abundant areas of scour and deposition. A scaled-down dynamic river would result in refreshed spawning gravels and re-invigorate geomorphic processes, with widespread removal of encroached vegetation along channel margins, and renewed floodplain establishment of cottonwoods and tree willows. System-wide changes resulting from ROD-specified management actions since 2000 have been modest and, in most cases, subtle. These smaller-than-expected changes triggered adaptive management to develop hypotheses and management actions to assess why larger changes were not occurring. Shortly after the implementation of the ROD, annual flow release planning began to incorporate flow requirements to achieve vegetation goals.

Annual flow release timing relied on qualitative seed dispersal periods described in the TRFE. To support flow timing that would promote black cottonwood establishment, seed dispersal timing was monitored in the Project Reach in WY 2004. Seed dispersal was quantified to compare the consistency of seed dispersal timing and investigate potential environmental factors affecting timing. The 2004 quantitative study corroborated the qualitative seed dispersal window identified in the TRFE.

In WY 2006, an adaptive management experiment using managed streamflow releases was implemented to encourage black cottonwood recruitment on upper bar surfaces and newly constructed floodplains at Hocker Flat (HVT and M&T 2007). The WY 2006 managed streamflow hydrograph was specifically developed to achieve cottonwood establishment. The hydrograph recession timing coincided with previously defined qualitive seed dispersal periods. The field experiment was coupled with germination, inundation and root growth experiments conducted in a lab. The cottonwood seed dispersal period used to schedule hydrograph recession in WY 2006 was inaccurate and seeds were not available at the Hocker Flat site as early as predicted. Field experiments were modified, and seeds were brought in from other locations in the watershed to conduct field seed germination experiments (HVT and M&T 2007).

The WY 2006 adaptive management experiment provided two lessons. The first lesson was that cottonwood and willow seeds need at least 21 days of constantly available soil moisture to grow large enough to withstand streamflow recession and have the energy to grow roots (at an average rate of 2.5 cm/day) to follow declining groundwater. The second lesson was that without quantitative cottonwood seed dispersal periods, we were likely to incorrectly target managed streamflow hydrographs and thus not be able to meet the soil moisture requirements needed for successful cottonwood seedling establishment.

To meet the 21-day soil moisture criterion, 3- to 5-day “flow benches” were recommended in WY 2010, 2011, and 2012 (Krause 2012, TRRP 2012). Bench duration and magnitude were dependent on water year type and were able to saturate soils to provide soil moisture conditions that would support root growth during the receding limb. The 3- to 5-day benches (e.g., 169.9 cms during wetter years) were intended to promote seed germination on upper bars and floodplains and were punctuated by a receding limb that maintained a 2.5 cm/day river streamflow water surface elevation drop at the downstream-most gage above the North Fork Trinity River. The combination of benches and slow recession was based on lessons learned in WY 2006 and recommended to provide adequate soil moisture to germinating seedlings (Mahoney and Rood 1998, HVT and M&T 2007).

Flow benches were expected to improve the performance of ROD streamflows in promoting cottonwood regeneration. The flow benches and gradual receding limbs require additional water volume, which is "expensive" in terms of available water for a given year and other restoration objectives trying to be achieved with its use. Limited quantities of cottonwood seedling establishment in 2011 and 2012 prompted re-evaluation of underlying assumptions, such as available seed trees and seed dispersal timing in the 64-km "Project Reach," which extends from Lewiston Dam downstream to the North Fork Trinity River (Figure 1).

To better develop flow releases that were appropriately timed to black cottonwood seed dispersal, additional seed dispersal monitoring occurred at several locations throughout the Project Reach between 2015 and 2018. It was thought that perhaps the TRFE and the 2004 dispersal study were limited by sample size, and that perhaps seed dispersal timing varied by water year type or other factors. Data collected between 2015 and 2018 have been used to fine-tune the seed dispersal period used during annual flow release planning. Black cottonwood seed dispersal periods from all monitoring years were evaluated together so that future recommendations for timing of spring releases could better coincide with black cottonwood seed dispersal. Potential environmental factors, such as heat accumulation (i.e., degree-hour) and day length (i.e., photoperiod) were evaluated as potential causal factors for seed dispersal timing in black cottonwood on the Trinity River. Potential sources of variation within the data were investigated to determine the reliability of a defined seed dispersal window. If the defined seed dispersal period was not reasonably consistent from year to year, it would be difficult to schedule flows appropriately to be able to meet objectives defined in the TRFE and ROD.

3 GOALS AND OBJECTIVES

The goal of the black cottonwood seed dispersal synthesis is to quantify the seed dispersal period within the Project Reach that can be consistently applied during annual flow scheduling so that the timing of key flow benches (e.g., 169.9 cms) coincides with cottonwood seed release. To meet this goal, this synthesis report has three primary objectives:

1. Determine if seed dispersal timing significantly differs between individual trees, between sites, and/or between years;
2. Define a seed dispersal period that can consistently be applied year to year, or describe why it is not possible to define a consistent seed dispersal period; and
3. Examine the relationship of time (e.g., calendar day, Julian day, Julian week, etc) and accumulated degree-hours with seed dispersal timing.

4 METHODS

Black cottonwood phenology has been documented twice in the Project Reach as described above in Section 2. Two separate seed dispersal monitoring efforts were undertaken (2004 and 2015–2018), and each effort used a different methodology. The difference in methodologies has led to difficulties in making meaningful comparisons during annual reporting (HVT and MA 2016, HVT and MA 2017, HVT and MA 2018). The analyses and results below focus on 2015–2018 data, but also incorporate 2004 data where appropriate.

Monitored phenological stages included bud break, flowering, capsule formation, and seed dispersal. Seed dispersal is defined as the period when capsules have opened to release hair-tufted seeds. Seed dispersal generally occurs over a 6-week period, which is short in terms of yearly timescales, but is too long to use during annual flow release planning. Peak streamflows are typically released from Lewiston Dam over 1–3 days and recede to summer baseflows by the end of July. Determining the best timing of peak streamflows to coincide with cottonwood seed dispersal requires a shorter seed dispersal "target" period, when the occurrence of cottonwood seed dispersal, regardless of volume, is almost certain. The methods below describe how the broad seed dispersal period was narrowed down into a target seed dispersal period.

4.1 2004 Study

The 2004 study design was based on preliminary investigations, specifically seed dispersal periods, that were conducted as part of the TRFE (M&T 1997, USFWS and HVT 1999, Bair 2001). Seed dispersal at six female trees was monitored starting in April 2004 at two locations: Bell Gulch (Rkm 135.1) and Junction City (Rkm 128.1). In WY 2004, black cottonwood phenology was evaluated once a week using seed traps and visual estimates of fruiting and seed release. Data from WY 2004 consisted of number of seeds collected on seed traps and visual canopy estimation of capsule formation and seed dispersal (flowering was not monitored). The visual observation data of estimated canopy cover were collected for the entire canopy and recorded using a categorical Daubenmire scale (i.e., 1=0–5%, 2=6–25%; 3=26–50%; 4=51–75%; 5=76–95%; 6=96–100%). It is likely that the five trees monitored at Junction City in 2004 were monitored again during the 2015–2018 study, but documentation in 2004 was not adequate to determine exact tree location.

4.2 2015–2018 Study

Seed dispersal was monitored at five sites starting in March in WY 2015–2019: (1) Lewiston, (2) Lowden Ranch, (3) Indian Creek, (4) Douglas City near Weaver Creek, and (5) Lower Junction City (Figure 1, Appendix A). Tree selection was based on several criteria: they had to be mature (i.e., reproductive), among the largest cottonwoods at a site, accessible to monitoring at all flows, and easily visible following leaf flush. A total of 39 female trees have been monitored since 2015 at these five sites. The sample size (i.e., number of trees) monitored at each site was different (Table 1) depending on the year. In WY 2015–2018, black cottonwood phenology was evaluated once a week using visual continuous estimates (vs. categorical as used in 2004) of flowering, fruiting, and releasing seeds. A fixed point was established from which to observe and record each female's phenological state (i.e., flowering, forming capsules, releasing "cotton"). Observations were made using standard binoculars and visually dividing each tree canopy into three segments (upper, middle, and lower). The number of open catkins (i.e., flowering) and whole capsules (i.e., fruit formation without seed dispersal) observed in each canopy segment in a 20-second sampling period was recorded, for a total of three observations per tree per visit. In addition, the percentage of capsules with cotton (i.e., fruits dispersing seeds) were visually estimated for the entire tree (one observation per visit). Study reaches were visited weekly on the same day each week (e.g., Lewiston on Monday, Douglas City on Tuesday, etc.) over the March–July monitoring period.

Table 1. Number of observations for each tree during each year. Final sample size to determine target seed dispersal period was 39.

Site	RKm	Tree ID	2004	2015	2016	2017	2018
Bell Gulch	135.1	1	19	0	0	0	0
Lower Junction City	128.1	1*	19	0	0	0	0
		2*	19	0	0	0	0
		3*	19	0	0	0	0
		4*	19	0	0	0	0
		5*	19	0	0	0	0
		566	0	11	0	0	0
		575	0	11	0	0	0
		JC A	0	11	14	18	15
		JC B	0	11	14	18	15
		JC C	0	11	14	18	15
		JC D	0	11	14	18	15
		JC E	0	11	14	18	15
		JC F	0	11	14	18	15
		JC Ga	0	11	14	18	15
		JC Gb	0	0	14	18	15
		JC H	0	0	14	18	15
		JC I	0	11	14	18	15
		JC J	0	11	14	18	15
Douglas City	152.8	DC01	0	11	14	18	15
		DC02	0	0	14	18	15
		DC03	0	11	14	18	15
		DC04	0	11	14	18	15
		DC05	0	11	14	18	15
		DC06	0	11	14	18	15
Indian Creek	153.2	584	0	11	0	0	0
		IC02	0	11	14	18	15
		IC03	0	11	14	18	15
		IC04	0	11	14	18	15
Lowden Ranch	168.1	LR01a	0	0	14	18	15
		LR01b	0	0	14	18	15
		LR01c	0	0	0	18	15
		LR01d	0	0	0	18	0
		LR02	0	0	14	18	15
		LR03	0	0	14	18	15
		LR04	0	11	14	18	15
Lewiston	179.9	500	0	11	0	0	0
		501	0	11	0	0	0
		502	0	11	0	0	0
		503	0	11	0	0	0
		506	0	11	0	0	0
		508	0	11	0	0	0
		LW01	0	11	14	18	15
		LW02	0	11	14	18	15
		LW03	0	11	14	18	15

* Trees monitored in 2004 at Junction City were likely monitored again in 2015–2018; 2004 tree location could not be verified due to inadequate field documentation.

4.3 Statistical Analysis

Seed dispersal data were assessed for normalcy and distribution (e.g., mean, standard deviation, etc.). Simple line plots were constructed showing seed dispersal as a function of date. Additional analyses were conducted to further explore relationships in the data as described below. All data analyses were conducted using Program R (R Core Team 2019).

4.3.1 Data Used for Analyses

The original data were estimates of percent seed dispersal of individual trees, or the percent of a tree canopy that was dispersing seeds on each monitoring date during the seed dispersal window. Initial analyses focused on comparisons between the 2015–2018 data, when methods were similar. A preliminary review of the data collected during seed dispersal monitoring (Section 4.2) identified that one of the trees was a low-functioning female, so the data for that tree were removed. Of the seed dispersal data collected during monitoring, we used the estimates of whole tree dispersal (i.e., the percent of a tree that was dispersing seeds) for the analyses in this report. We refer to these data as original seed dispersal data throughout the report. From the original seed dispersal data, we developed three separate data types used in the analyses as well. These date types are: (1) median seed dispersal, (2) peak seed dispersal, and (3) a binary indicator of seed dispersal (Table 2). Median seed dispersal is the median seed dispersal value of all trees per survey week (1 data point per week per year). Peak seed dispersal is the first Julian date when an individual tree had greater than or equal to 75% of the canopy dispersing seeds in each year (1 data point per tree per year). The binary indicator of seed dispersal is the original seed dispersal data simplified to 1 or 0 values depending if seed dispersal was occurring (1) or not occurring (0).

Table 2. Data type terms, their definitions, the statistical test or analysis approach used for each data type, and purpose of test used in the seed dispersal analyses.

Data Type Term	Definition	Data Format	Statistical Test or Approach	Hypotheses Tested
Original seed dispersal data	Raw data, the percent of each tree canopy that was dispersing seeds in each survey week.	Multiple data points per week per year	Scatter Plots	H_0: There is no relationship between percent seed dispersal and accumulated degree-hour.
Median seed dispersal	The median percent dispersal value of all trees in each survey week	1 data point per week per year	Line Charts	H_0: There is no relationship between median percent seed dispersal and accumulated degree-hour.
Peak seed dispersal	The Julian date when a tree has greater than or equal to 75% dispersal in each year.	1 data point per tree per year	Scatter Plots Box Plots	H_0: Timing of the beginning of peak seed dispersal (≥ 75% canopy dispersing) does not differ between years, sites, and/or trees.
Binary seed dispersal	Indicator of seed dispersal data represented by 1 if seed dispersal was occurring and a 0 if not occurring.	Multiple data points per week per year	Kruskal-Wallis Rank Sum Test	H_0: Seed dispersal timing (i.e., start, duration, and end) does not differ between years, sites, and/or trees.
		Multiple data points per week per year	Generalized linear model (GLM)	H_0: Timing of seed dispersal (i.e., start, duration, and end) cannot be predicted by years, sites, trees, Julian data, and/or accumulated degree-hours.

WY 2004 data were collected using a different field method, and the categorical format of the 2004 data required additional transformation before they could be compared with the 2015–2018 data. The 2004 data were converted to binary seed dispersal data (Table 2) and were used in analyses comparing differences between trees and for comparisons at Junction City, where additional years of monitoring data were available. The original 2004 data were included in the simple line plot showing seed dispersal as a function of time but were not used during the development of a predictive model.

In addition to the seed dispersal data (response variable), other variables accounted for in the analyses included individual trees, sites, years that sites were surveyed, Julian date of each observation, and accumulated degree-hour (accumulated hour). These data were used as predictor variables in the analyses. Julian date is a continuous count of days within a year and accounts for the variation in length between typical years and leap years.

Plant growth and development from one stage to the next (i.e., winter dormancy to bud break, bud break to flowering, flowering to seed formation, etc.) have been shown to be influenced by air temperature (Stella et al. 2006, Schröder et al. 2014). Temperatures must occur between a minimum and maximum value for flower development to progress to the next stage; temperatures below the minimum or above the maximum will halt development. Heat accumulates over time (i.e., day after day), and once a given threshold is reached, development progresses to the next stage. The total amount of heat over time needed to move a plant from one stage to the next is measured in units called degree-hours.

Accumulated degree-hour is a way to measure the passage of time and the accumulation of temperature simultaneously. The accumulated sum of hourly temperature measurements above a specified threshold is summed daily, and the daily values are added to determine the accumulated degree-hours. The total number of daily accumulated degree-hours above the threshold was used in the analysis.

The temperature selected as the threshold can influence the results of degree-hour accumulation because degree-hours will accumulate faster from a lower threshold. U.C. Davis provides a degree-hour calculator () online. Air temperatures from the California Data Exchange Center (CDEC) Lewiston (LWS) Station Sensor 4 were downloaded for WY 2015–2018 and used as input for the degree-hour calculator. The minimum temperature was set to 4.4 °C (40 °F), but a maximum temperature was not set, as capsule dehiscence likely continues at high air temperatures.

We previously compared a 4.4 °C (40 °F) and a 10 °C (50 °F) minimum threshold based on the assumption that soil becomes biologically active when it is 10 °C or warmer, and that this would biologically relate to root growth and nutrient uptake, bud swell, flowering, and leaf flush. The comparison showed that the lower threshold (4.4 °C) accumulated degree-hours faster, but that the shape of the curves for each threshold were similar. For this analysis, we chose a minimum temperature threshold of 4.4 °C because the number of degree-hours above 4.4 °C begins to accumulate sooner and faster, which better informs management decisions earlier in the year, during the development and scheduling of ROD flows. If degree-hours are the main factor influencing black cottonwood seed dispersal timing, seed dispersal should begin sooner in hotter years. If, however, other factors exert more influence on seed dispersal timing, seed dispersal timing should be consistent, regardless of air temperatures in a given year. Numerous other environmental factors may influence seed dispersal timing, such as site-specific relative humidity, wind speed, precipitation, vernalization, and soil moisture (Braatne et al. 1996, Stella et al. 2006, Cao et al. 2009, Herbison et al. 2015). However, the sites occur in a remote, mountainous river and site-specific environmental data were not collected as part of this dispersal timing synthesis report. Instead, existing air temperature data from the National Oceanic and Atmospheric Administration Lewiston climate station were used in the analyses.

4.3.2 Summary of Statistical Approach

Seed dispersal timing and its underlying causes were evaluated using various statistical methods (Table 2). During the development of the WY 2018 seed dispersal synthesis workplan (Appendix B), it was anticipated that analysis of variance (ANOVA) would be used to compare timing of seed dispersal between all the years monitored (i.e., 2004, 2015–2018). However, an important assumption of ANOVA is that the data follow a normal distribution (i.e., bell-shaped curve). The seed dispersal data were not normally distributed nor could the data be transformed to meet normality assumptions because there were many 0 values that were real data points (i.e., seed dispersal was not occurring yet or had already completed). Therefore, the non-parametric equivalent Kruskal-Wallis Rank Sum Test was performed in place of an ANOVA analysis. A Kruskal-Wallis rank sum test was applied to the binary seed dispersal data to test whether the probability of seed dispersal was different among trees, years, and sites. If a test was significant ($p \leq 0.05$), a post hoc analysis was conducted to test which relationship within a variable (i.e., tree 1 vs tree 2 of all trees, or 2015 vs 2018 of all years) had the most significant effect on the probability of seed dispersal. Box plots were constructed to visually compare the timing (Julian date) of peak seed dispersal among trees, years, and sites, and among sites within years. Line charts were used to observe the yearly relationship between median percent dispersal and accumulated degree-hours.

A generalized linear model (GLM) for a binomial distribution was used to develop the best statistical relationships between seed dispersal occurring (response variable) and the variables that best predicted seed dispersal occurring (predictor variables) to predict the timing of the highest probability of seed dispersal occurring in any year. Since the data were not normally distributed, a GLM was determined to be appropriate because generalized linear models do not assume response variables follow a normal distribution as a traditional linear model would. A binomial distribution was used because there was a fixed number of observations, each observation represented one of two outcomes (seed dispersal occurring or not occurring), and the probability of seed dispersal occurring was the same for each observation. The binomial distribution requires that observations are independent; however, our observations were made on the same trees over time. Akaike Information Criterion value (AIC, Burnham and Anderson 2002) was used to select a GLM with variables that best fit the binary seed dispersal data. The AIC method selects the best fit model by removing predictor variables one at a time until only the predictor variables that best predict the response variable are left.

5 RESULTS

General timing of phenological stages was visually compared by plotting each year's original data (Table 2) against time (Figure 3, Figure 4). Flowering began consistently in all years when flowering was monitored (2015, 2016, 2017, and 2018), except 2018 (see orange line in Figure 3). In 2018, flowering began almost two weeks later than in 2015, 2016, and 2017. Capsule formation continued through early June, which corresponded to the approximate end of seed dispersal. WY 2017 had the longest flowering/capsule formation period, which lasted about 11 weeks (red line in Figure 3).

Seed dispersal occurred during a similar period in all monitored years (Figure 4). Between April 19 and July 3, 100% of seed dispersal at every tree and site had occurred. The timing of seed dispersal in WY 2004, WY 2015, and WY 2016 was almost identical, beginning around April 19 and ending around June 10. The timing of seed dispersal in WY 2017 and WY 2018 occurred later and was not as similar between the two years (Figure 4). Of all the years measured, the seed dispersal period in WY 2017 started the latest, ended the latest, and was the longest. Additionally, the maximum number of trees dispersing seeds during a given week was lowest in WY 2017 (only 80% of trees, Figure 4). However, individual trees were observed to have 100% of their capsules dispersing seeds in WY 2017; no other years were observed to have such a high percentage of seed dispersal per tree during a single week, even though all trees were observed to be dispersing.

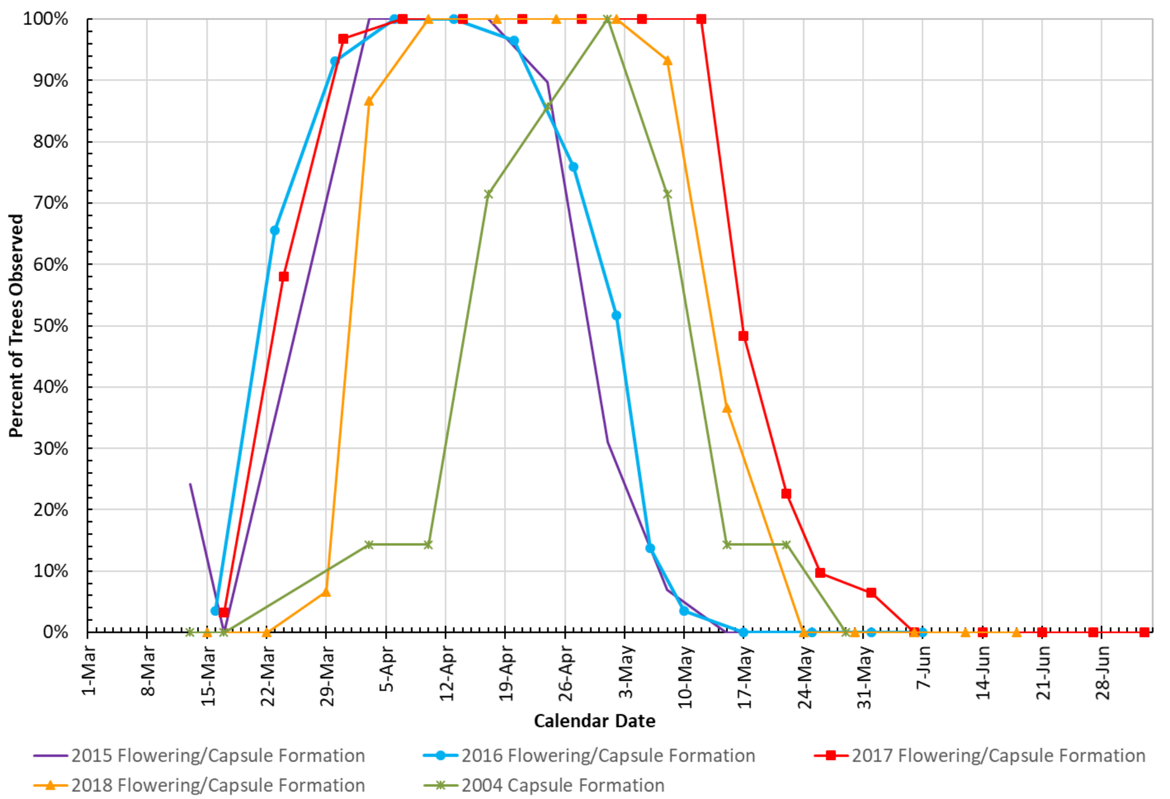

Figure 3. Percent of trees flowering and/or forming capsules during all years monitored. During 2004, flowering was not monitored, which could account for the later start time.

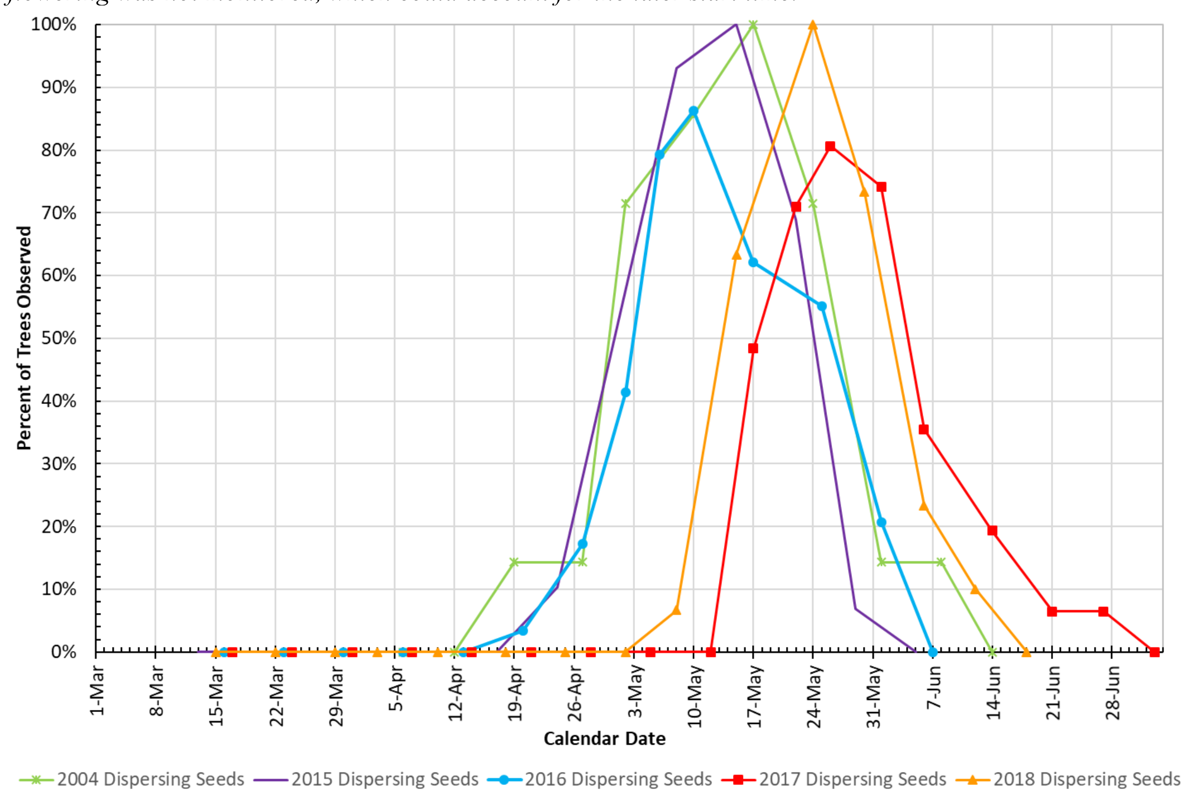

Figure 4. Percent of trees dispersing seeds each week for during all years monitored. Note that all seed dispersal occurs between April 19 and July 3.

In previous years, the seed dispersal window has been identified by the beginning date, a period of peak dispersal, and the end date (HVT and MA 2015, HVT and MA 2016, HVT and MA 2017). As discussed earlier, a seed dispersal window of April 19 to July 3 is too broad to be useful during annual flow release planning, because peak releases occur over only a few days. Releases and the subsequent receding limb need to coincide with the timing of when most cottonwood seeds are being dispersed to successfully promote black cottonwood establishment (Figure 5). Five years of monitoring data showed that seed dispersal sometimes occurs earlier within this broad window (e.g., 2004, 2015, 2016), and sometimes later (2017, 2018). This synthesis report further explored the variation in seed dispersal between trees, sites and years to evaluate whether a shorter target seed dispersal period could be defined and consistently applied regardless of water year type.

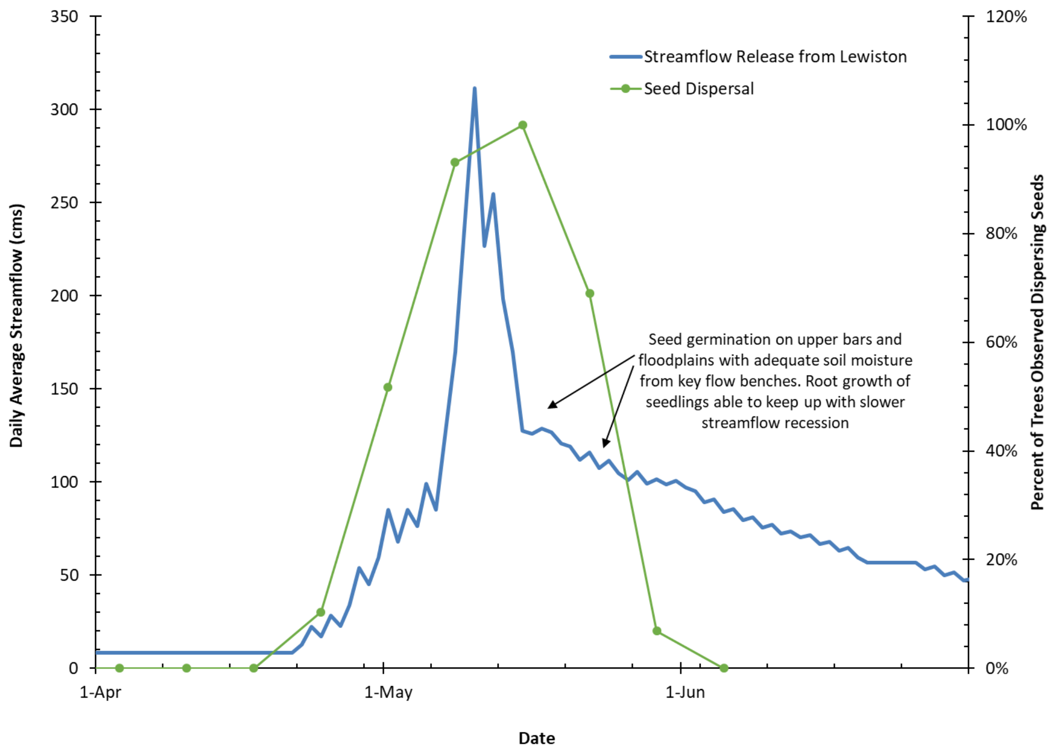

Figure 5. Conceptual drawing showing the timing of streamflow releases in relation to black cottonwood seed dispersal to achieve germination and establishment on upper bars and floodplains.

5.1 Variation Between Trees, Sites, and Years

A Kruskal-Wallis rank sum test on the binary data indicated that the probability of seed dispersal occurring on a given date was only different between years (Table 3). The probability of seed dispersal between trees or between sites did not differ. A post hoc test suggested that most between-year probabilities of seed dispersal were different ($p \leq 0.05$), except between 2015 and 2016, and 2017 and 2018, where probabilities of seed dispersal were similar (Table 4).

Table 3. Kruskal-Wallis rank sum test results of differences in seed dispersal between trees, years, and sites. A p-value ≤ 0.05 indicates a significant difference of seed dispersal response.

Variables	Chi-squared	Degrees of Freedom	P-value
Trees	25.90	38	0.93
Years	18.72	3	≤ 0.05
Sites	7.74	4	0.10

Table 4. Results of a post-hoc analyses testing which years had the most significant difference in the probability of seed dispersal.

Year	P–value			
	2015	**2016**	**2017**	**2018**
2015	–	–	–	–
2016	0.23	–	–	–
2017	< 0.05	< 0.05	–	–
2018	< 0.05	< 0.05	0.38	–

Scatter plots showing the date of peak seed dispersal for individual trees indicated that peak seed dispersal occurred on a later Julian date in 2017 and 2018 compared to 2015 and 2016 (Figure 6). The scatter plots corroborate the dispersal trend shown in Figure 4.

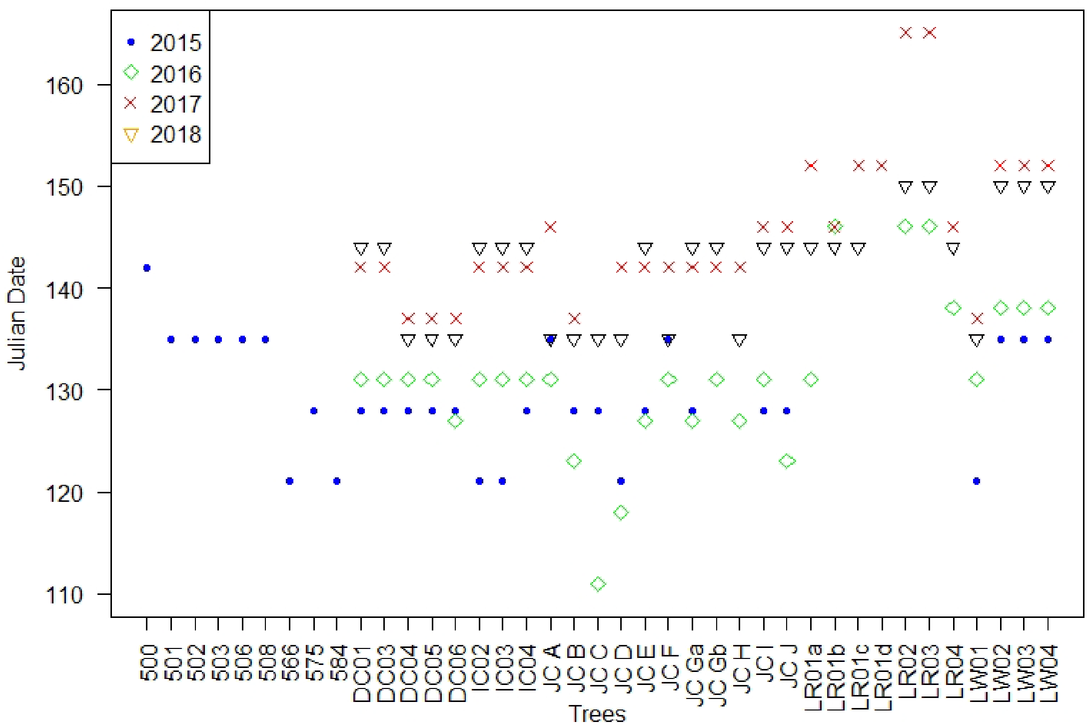

Figure 6. Julian date of peak dispersal (Table 2) for each tree surveyed during each survey year. Julian day 110=April 19, 120=April 29, 130=May 9, 140=May 19, 150=May 29, 160=June 8 during a non-leap year.

A post hoc power analysis was conducted to determine whether we had a large enough sample size to be able to detect differences between groups (Table 5). Power was set at 0.8 (80% chance of detecting differences that really exist), and a medium effect size of 0.25 was used (25% difference between groups). For groupings by site, to achieve a power of 0.8, and an effect size of 0.25, a sample size of 39 trees per site would be needed for 5 sites (195 trees total). Monitoring 39 trees per site in the Project Reach is problematic for several reasons, namely the lack of adult female cottonwoods and the prohibitive cost of monitoring such a large number of trees. For groupings by tree, each tree would need to be sampled for 11 years. For groupings by year, 45 trees for the entire Project Reach would need to be sampled for 4 years to achieve that same power and effect. Our four-year sampling included only 39 trees, so power to detect differences between years is likely less than 0.8 (Table 5). However, adding just one additional year of sampling (2019) would decrease the needed sample size to 39. The fact that a difference between some years was detected suggests that the difference is relatively large.

Table 5. Post hoc power analysis showing power and effect size of current data set.

Group Type	Number of Groups	Current Sample Size by Group	Power*	Effect**
Sites	5	Smallest = 3	0.08	1.12
		Largest = 11	0.25	0.48
Trees	39	4	0.22	0.46
Years	4	39	0.74	0.27

* With an effect of 0.25.

**With a power of 0.80.

Box plots of peak seed dispersal timing show that the median date of peak seed dispersal (not to be confused with the separate data set, median seed dispersal, Table 2), occurred progressively later and later each year when plotted by year (Figure 7). Box plots of peak seed dispersal timing of years at each site showed a similar trend to plots of individual trees and years, in that the median date of peak seed dispersal generally occurred later in the seed dispersal window for 2017 and 2018 compared to 2015 and 2016 (Figure 8). Box plots of peak seed dispersal timing by site showed that the median date of peak seed dispersal was generally around Julian date 135 (May 14) for Lewiston, Indian Creek, and Junction City, and later for Lowden, and earlier for Weaver Creek (Figure 9); however, these differences were not statistically significant.

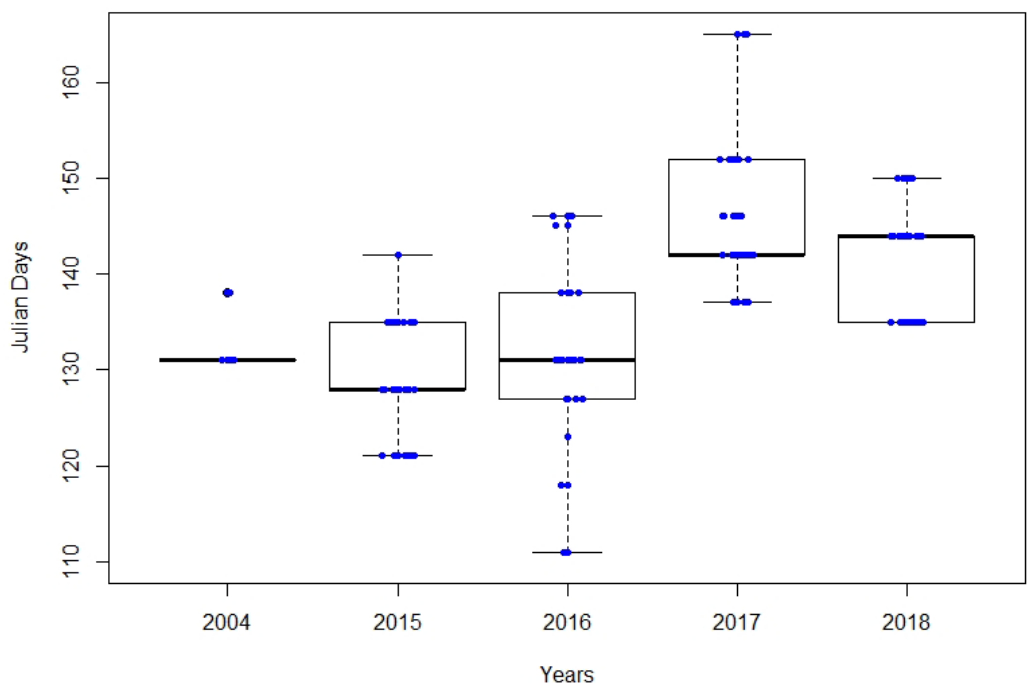

Figure 7. Box plots of Julian date when peak seed dispersal occurred during each year surveyed. Junction City was the only site monitored in 2004. Blue dots are the peak dispersal Julian date for an individual tree. The upper and lower limits of the box are the first and third quartiles (25th and 75th percentiles, respectively). The dark lines represent the median of peak seed dispersal timing, the whiskers are the bounds of the minimum and maximum values, unless the minimum or maximum values are out of interquartile range. Then the whiskers are the interquartile range and the blue dots are values outside of the interquartile range and considered outliers. Julian day 110=April 19, 120=April 29, 130=May 9, 140=May 19, 150=May 29, 160=June 8 during a non-leap year.

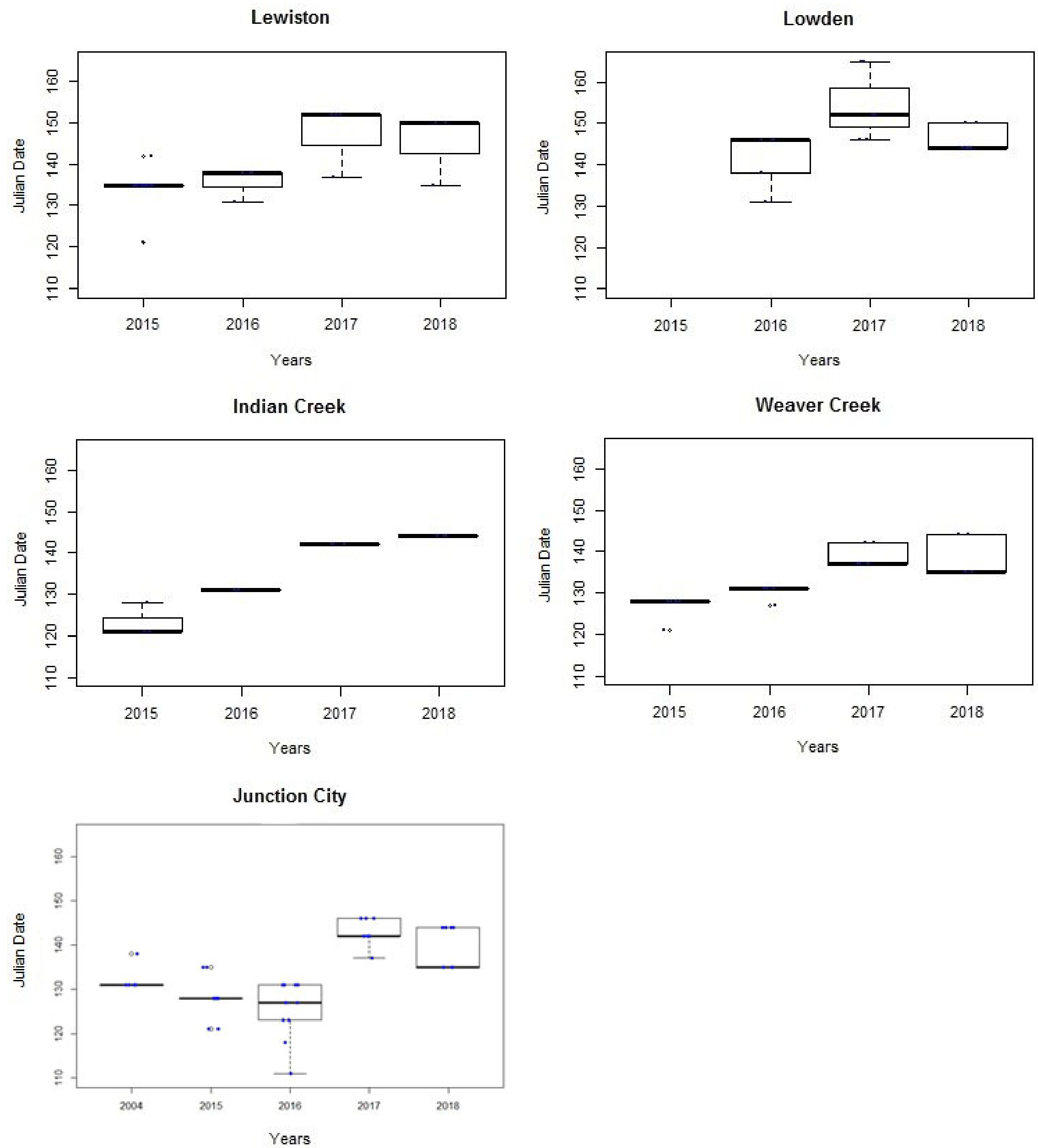

Figure 8. Box plots of Julian date when peak dispersal occurred during each year surveyed, separated by site. Junction City was the only site surveyed in 2004. Lowden was not surveyed in 2015. Julian day 110=April 19, 120=April 29, 130=May 9, 140=May 19, 150=May 29, 160=June 8 during a non-leap year.

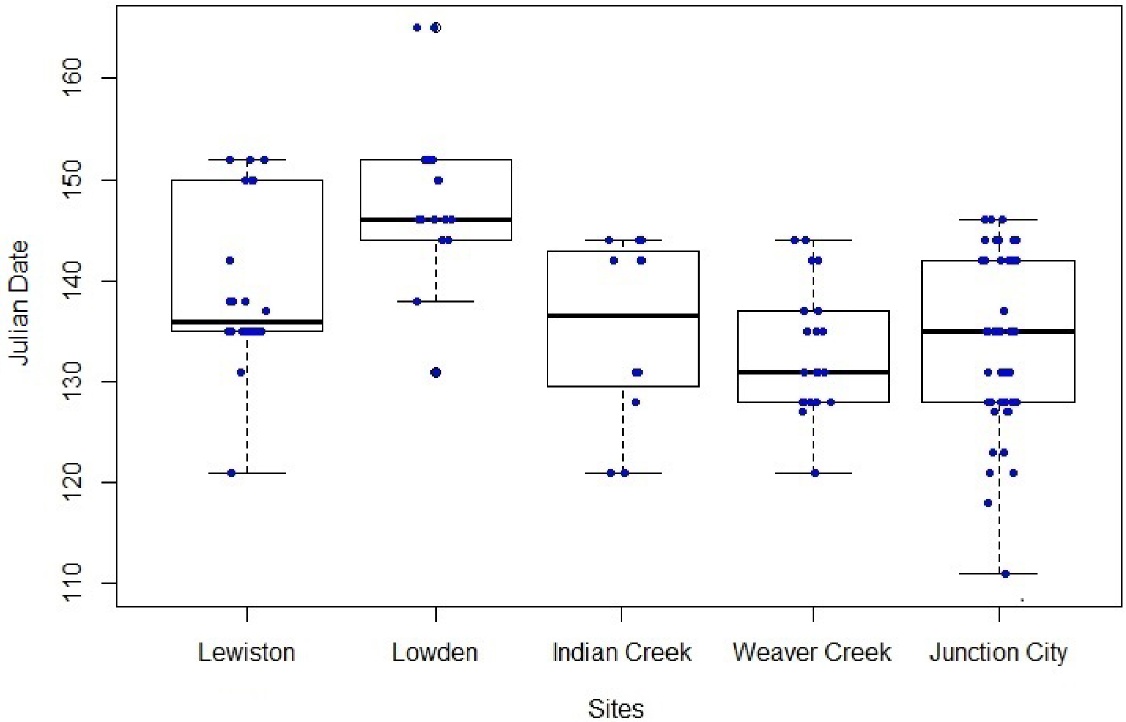

Figure 9. Box plots of Julian date when peak dispersal occurred at each site in WY 2015–2018. Blue dots are the peak dispersal Julian date for an individual tree. The upper and lower limits of the box are the first and third quartiles (25th and 75th percentiles, respectively). The dark lines represent the median of peak dispersal timing, the whiskers are the bounds of the minimum and maximum values, unless the minimum or maximum values are out of interquartile range. Then the whiskers are the interquartile range and the blue dots are values outside of the interquartile range and considered outliers. Julian day 110=April 19, 120=April 29, 130=May 9, 140=May 19, 150=May 29, 160=June 8 during a non-leap year.

5.2 Relationship Between Julian Date, Accumulated Degree-hours, and Seed Dispersal Timing

Air temperature is one factor that could affect the timing of seed dispersal between wetter and drier water year types. Presumably, drier water years are warmer earlier, leading to a faster accumulation of degree-hours. Percent seed dispersal for individual trees (original data) was plotted against accumulated degree-hours to observe between-year trends in dispersal rates related to air temperature (Figure 10). An obvious demarcation occurred at 2,000 accumulated degree-hours: seed dispersal did not occur before 2,000 accumulated degree-hours during 2015–2018 (Figure 10). When WY 2004 data were included in the plot, seed dispersal began around 1,700 accumulated degree-hours (Figure 11). When median seed dispersal was plotted against accumulated degree-hours, median percent seed dispersal occurred at approximately the same accumulated degree-hour for three of the four years; the 2015 peak in median seed dispersal occurred at a higher accumulated hour (Figure 12). WY 2015 occurred during California's 2012–2015 record-breaking drought, which consisted of the driest three consecutive years in measured history combined with extremely warm temperatures (Swain). However, although the degree-hours accumulated faster in WY 2015, the timing of seed dispersal remained approximately the same as in WY 2004 and WY 2016 (Figure 4). Interestingly, for all years, seed dispersal was nearly completed by the time 3,000 degree-hours had accumulated, regardless of when seed dispersal began (except a single measurement in WY 2017, see Figure 10).

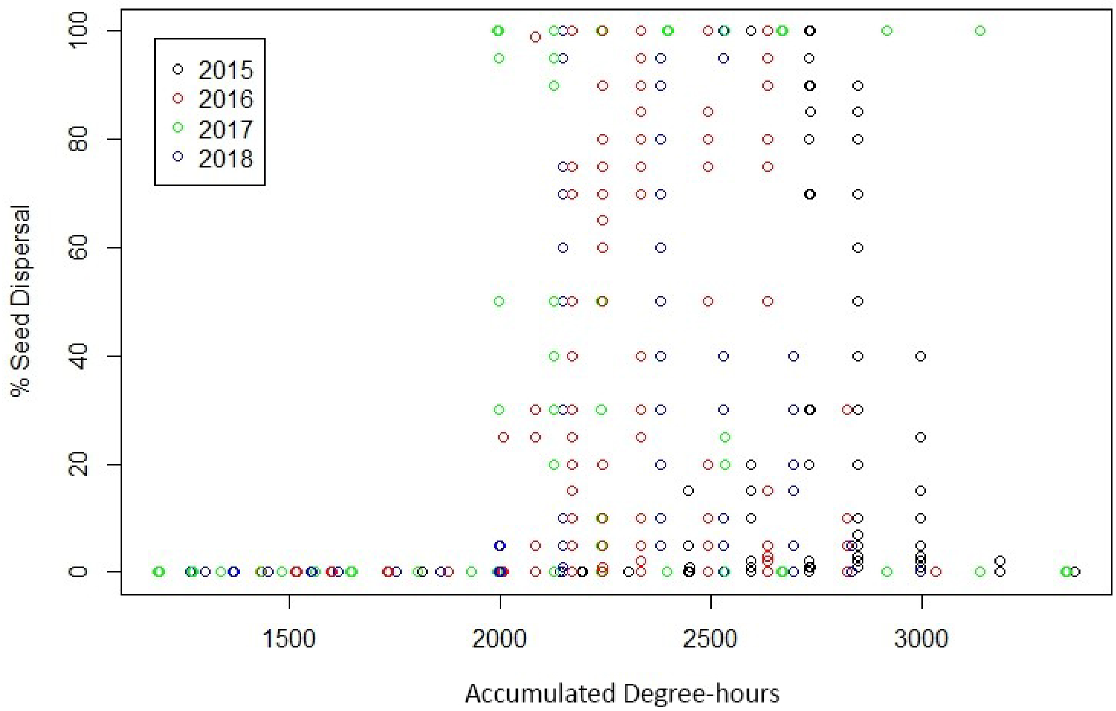

Figure 10. Plot of percent seed dispersal and accumulated degree-hours for WY 2015–2018. Seed dispersal did not occur prior to 2,000 accumulated degree-hours. Only a few samples were taken after 3,000 accumulated degree-hours because seed dispersal monitoring ended once seed dispersal was no longer observed. Circles are color-coded by year.

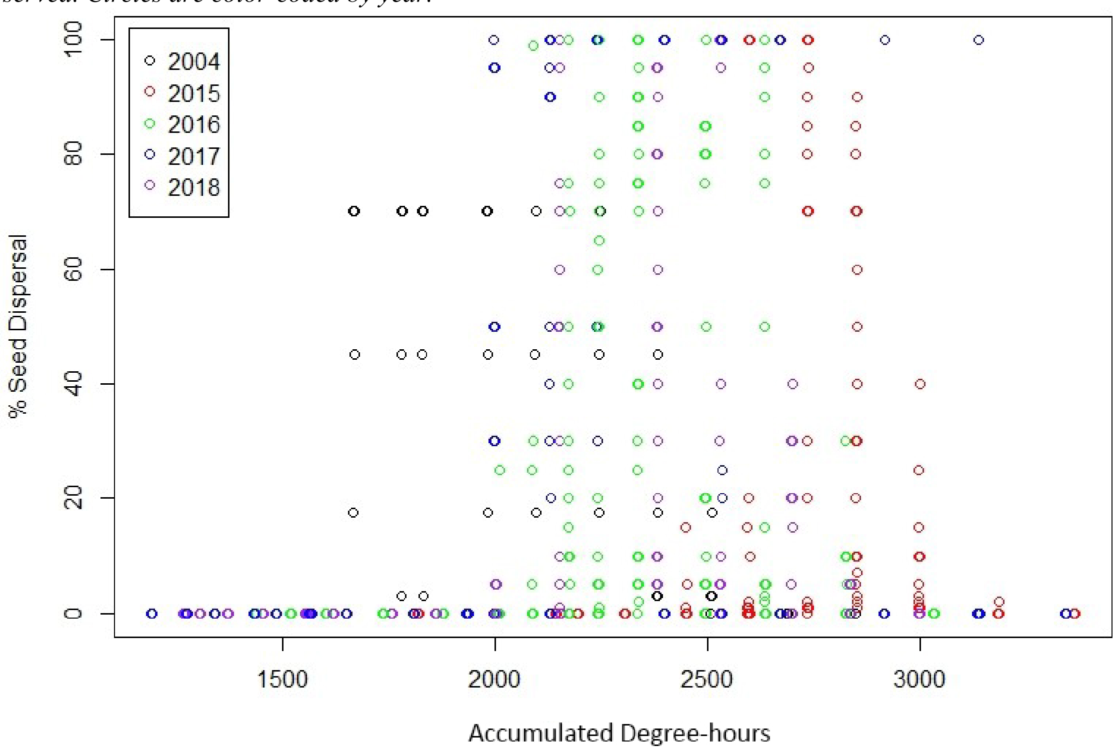

Figure 11. Plot of percent seed dispersal and accumulated degree-hours with WY 2004 data added. Note that seed dispersal began prior to 2,000 accumulated degree-hours in 2004. Only a few samples were taken after 3,000 accumulated degree-hours because seed dispersal monitoring ended once seed dispersal was no longer observed. Circles are color-coded by year.

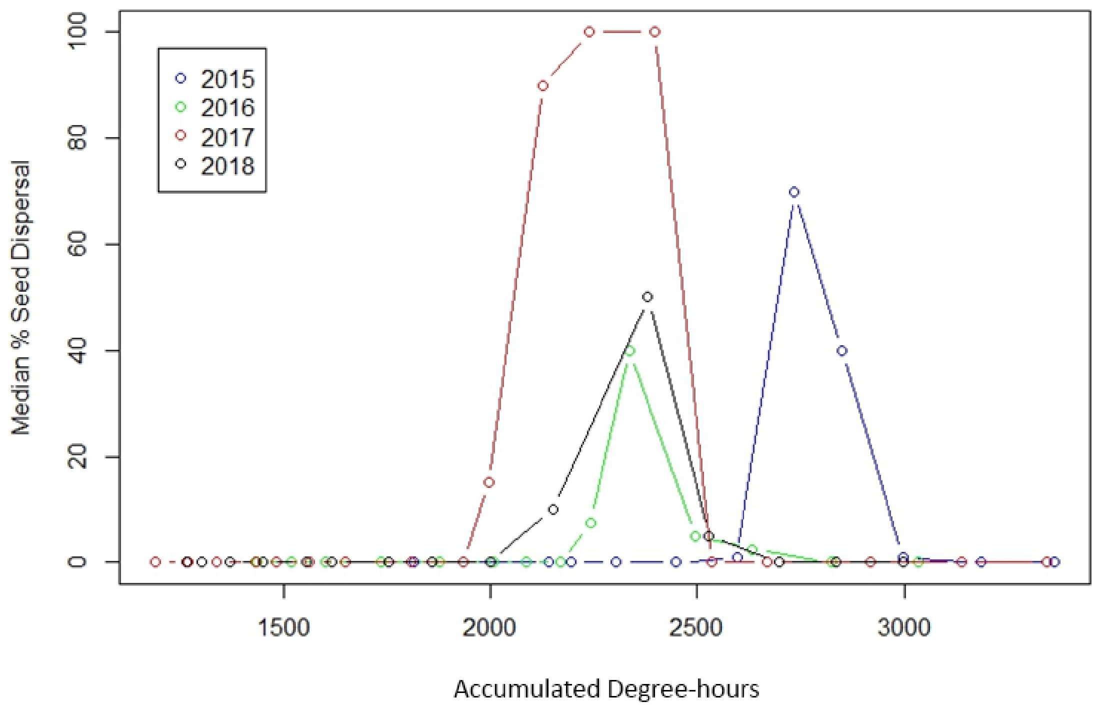

Figure 12. The median percent dispersal for each week in each year plotted against accumulated degree-hours.

Water year class does not show any apparent relationship to the peak seed dispersal timing within the same year; however, the water year class of the previous year may influence the seed dispersal periods of the following year (Table 6). Results from the simple line chart of seed dispersal (Figure 4) and the Kruskal-Wallis rank sum test (Table 3, Table 4) indicated that 2015 and 2016 were like each other but different from other years, and that 2017 and 2018 were like each other but different from the others. Dry water year classes preceded both 2015 and 2016, while wetter water year types preceded both 2017 and 2018 (Table 6). The influence of the previous year on the following year's seed dispersal makes intuitive sense because cottonwood trees develop flower buds during the growing season of the preceding year (Boes and Strauss 1994, Kaul 1994). One hypothesis to explain why preceding water year type influences seed dispersal timing is that if the preceding year is dry, a plant would have fewer available resources to devote to reproduction for the following year, with fewer flowers and catkins developing the following year. Fewer catkins and less reproductive energy could result in earlier seed dispersal. Conversely in wetter years, more energy and resources can be spent preparing for the following year's reproduction. In the following spring, it takes longer for the higher numbers of flowers and catkins to mature and the seed dispersal period is delayed. Climatic conditions presumably responsible for cuing the timing of seed dispersal also presumably reflect water year type. In other words, seed dispersal timing likely responds to a combination of climatic variables, and the relative influence of each variable likely shifts between water year types. Although we can deduce that water availability is a direct outcome of water year type, there are undoubtedly other factors that characterize differences between wetter and drier years (e.g., relative humidity, solar radiation, etc.).

Table 6. Calendar date (Julian date) when the median of peak dispersal (≥ 75% dispersal) occurred at each site for each year sampled, and the associated water year type.

Year	Water Year Classification	Water Year Classification of Preceding Year	Julian Date of Median Peak Dispersal				
			Lewiston	Lowden	Indian Creek	Weaver Creek	Junction City
2015	Dry	Critically Dry	May 14 (135)	N/A	Apr 30 (121)	May 7 (128)	May 7 (128)
2016	Wet	Dry	May 17 (138)	May 25 (146)	May 10 (131)	May 10 (131)	May 6 (127)
2017	Extremely Wet	Wet	May 31 (152)	May 31 (152)	May 21 (142)	May 16 (137)	May 21 (142)
2018	Critically Dry	Extremely Wet	May 29 (150)	May 23 (144)	May 23 (144)	May 14 (135)	May 14 (135)

N/A = Site was not sampled during survey year.

5.3 Defining a Target Seed Dispersal Period

For the 2015 to 2018 data, individual tree seed dispersal values for each week (original data) were ranked and the median value selected. Seed dispersal median values for all years combined were plotted against the survey weeks during the seed dispersal period. The highest median seed dispersal for all years combined occurred at survey week 11 (Figure 13), where corresponding survey dates for all years range from May 22 to May 26 (Table 7). Survey weeks 10 and 11 had the highest median seed dispersal, and seed dispersal for all trees always occurred during these two weeks. Therefore, the calendar dates corresponding to survey weeks 10 and 11 are recommended as the black cottonwood target seed dispersal period for annual flow release planning (May 15 to May 28).

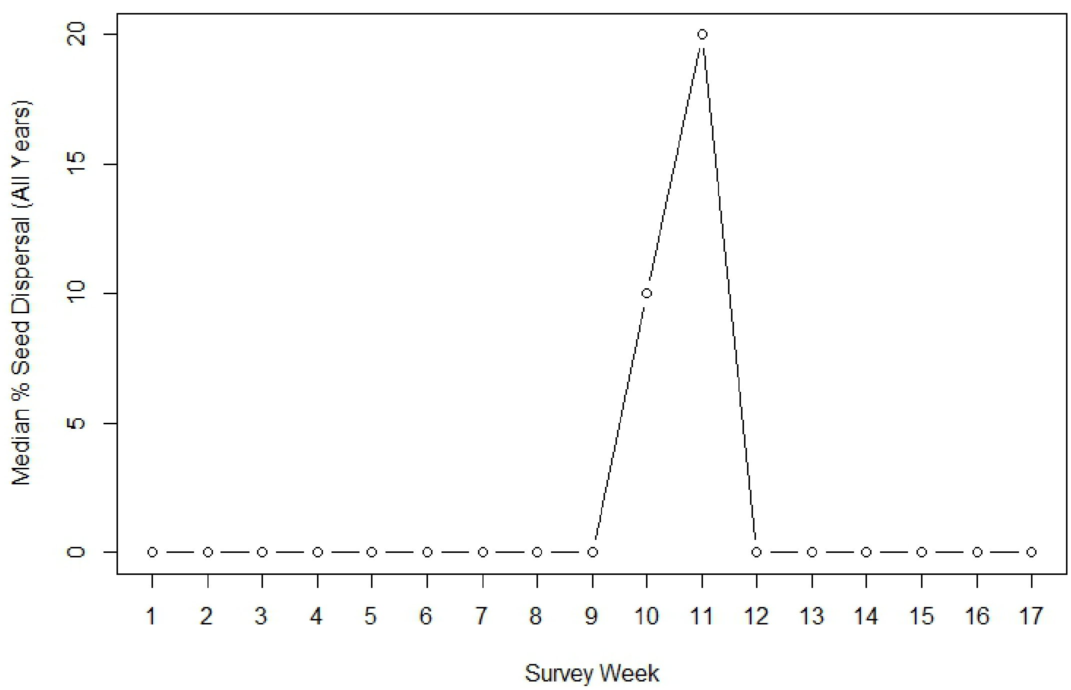

Figure 13. The median percent dispersal of each week for all years combined plotted against survey week. See Table 7 for dates of each survey week for each year.

Table 7. The calendar date associated with the survey week for each year surveyed. Week 11 (highlighted in green) had the highest median dispersal for all years combined.

Survey Week	2015	2016	2017	2018
1	3/13/2015	3/16/2016	3/17/2017	3/15/2018
2	N/A	3/23/2016	3/24/2017	3/22/2018
3	N/A	3/30/2016	3/31/2017	3/29/2018
4	4/3/2015	4/6/2016	4/7/2017	4/3/2018
5	4/10/2015	4/13/2016	4/14/2017	4/10/2018
6	4/17/2015	4/20/2016	4/21/2017	4/18/2018
7	4/24/2015	4/27/2016	4/28/2017	4/25/2018
8	5/1/2015	5/2/2016, 5/6/16	5/5/2017	5/2/2018
9	5/8/2015	5/10/2016	5/12/2017	5/8/2018
10	5/15/2015	5/17/2016	5/17/2017	5/15/2018
11	5/22/2015	5/25/2016	5/22/2017, 5/26/17	5/24/2018
12	5/29/2015	6/1/2016	6/1/2017	5/30/2018
13	6/5/2015	6/7/2016	6/6/2017	6/6/2018
14	N/A	N/A	6/14/2017	6/12/2018
15	N/A	N/A	6/21/2017	6/18/2018
16	N/A	N/A	6/27/2017	N/A
17	N/A	N/A	7/3/2017	N/A

N/A: No survey was conducted for the week.

To compare how the recommended target seed dispersal period would have performed during the years monitored, seed dispersal was overlaid onto annual hydrographs (Figure 14, Figure 15, Figure 16, Figure 17). In the four years that were compared, the target seed dispersal period occurred during flow benches and coincided with the timing of the receding limb (Figure 18). In addition, the actual observed seed dispersal period overlapped almost entirely with the recommended target seed dispersal period. Even in WY 2017, when seed dispersal timing was so different from other years, the two periods overlapped well, with approximately half of the actual seed dispersal period in WY 2017 occurring within the target seed dispersal period. Moreover, the target seed dispersal period is well-placed within the broad seed dispersal window to capture earlier seed dispersal years (e.g., 2015, 2016) as well as later seed dispersal years (e.g., 2017, 2018).

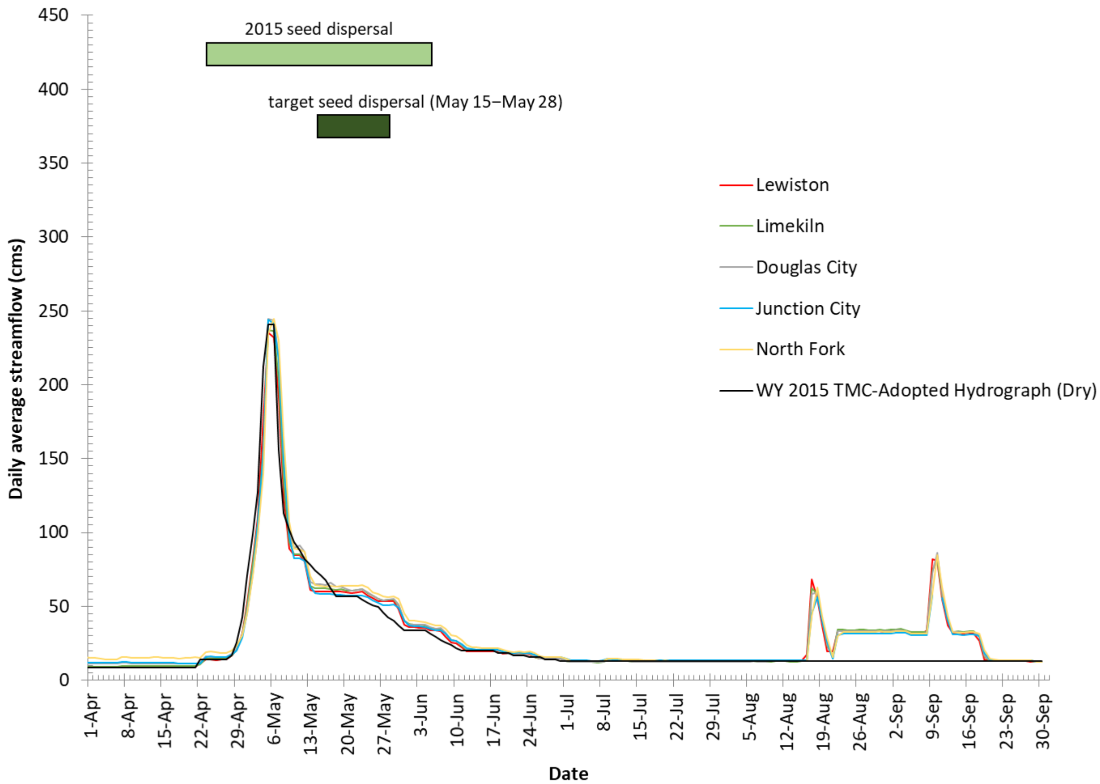

Figure 14. Annual WY 2015 hydrograph at five streamflow gages, with 2015 seed dispersal and recommended target seed dispersal periods overlaid.

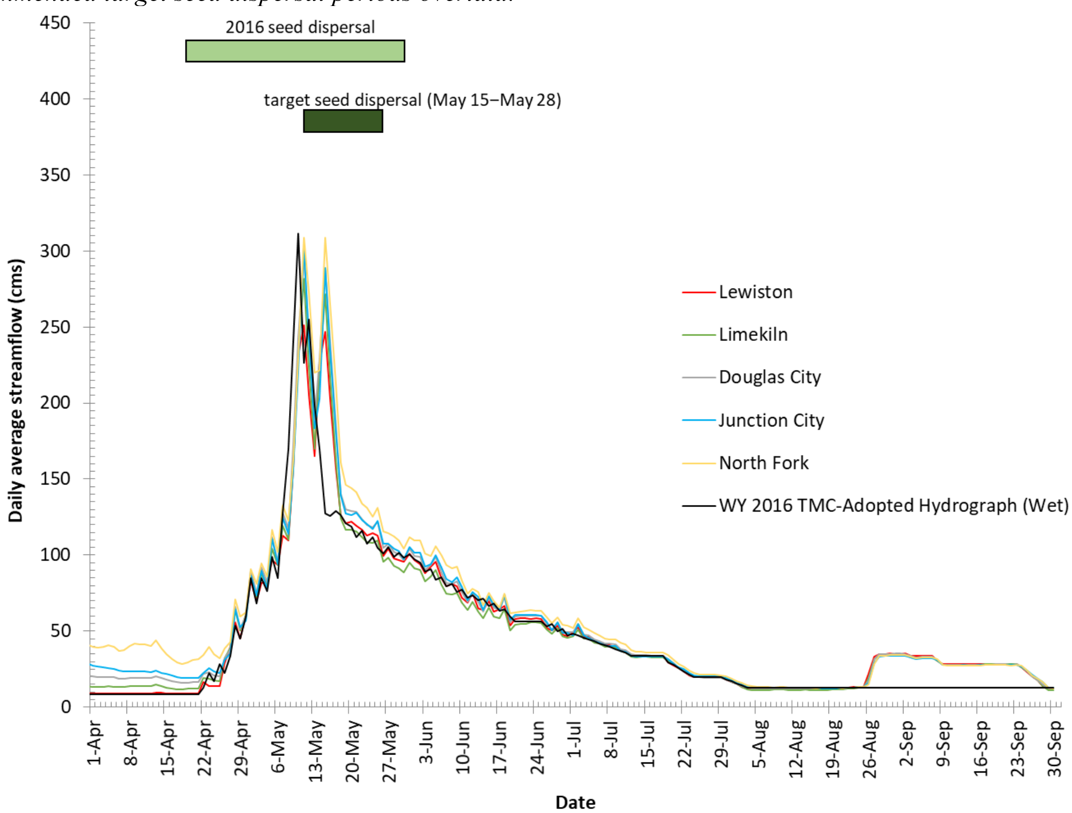

Figure 15. Annual WY 2016 hydrograph at five streamflow gages, with 2016 seed dispersal and recommended target seed dispersal periods overlaid.

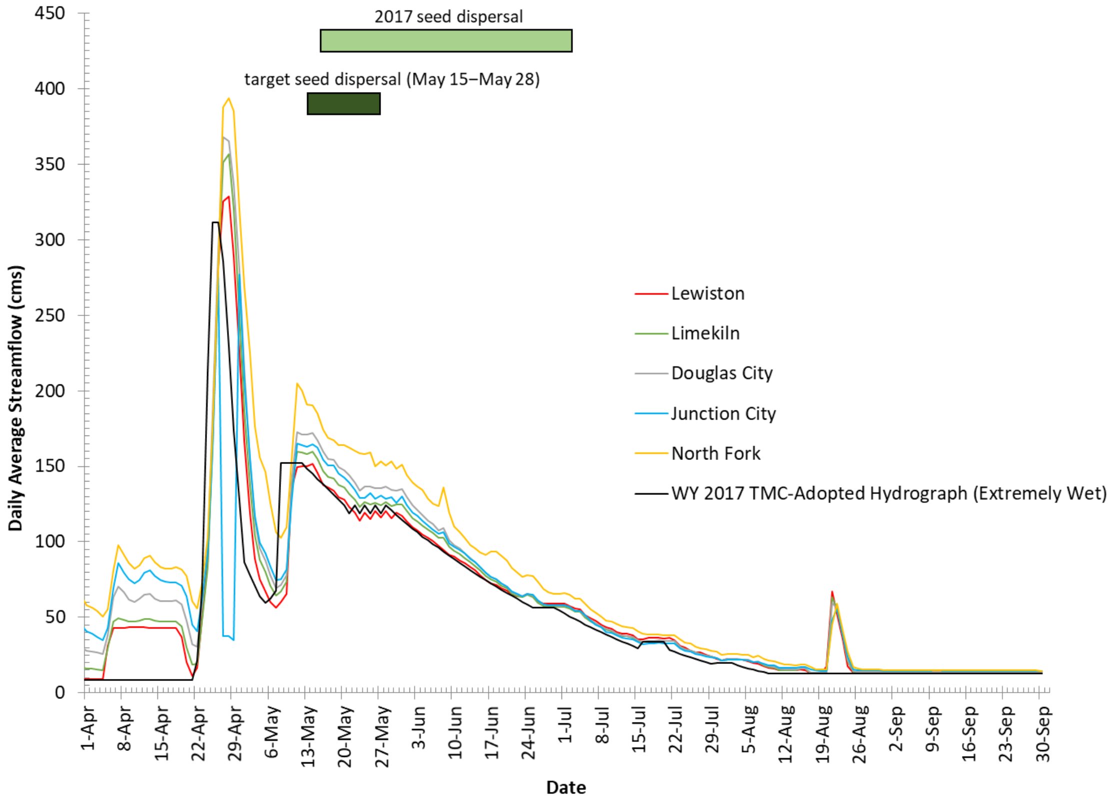

Figure 16. Annual WY 2017 hydrograph at five streamflow gages, with 2017 seed dispersal and recommended target seed dispersal periods overlaid.

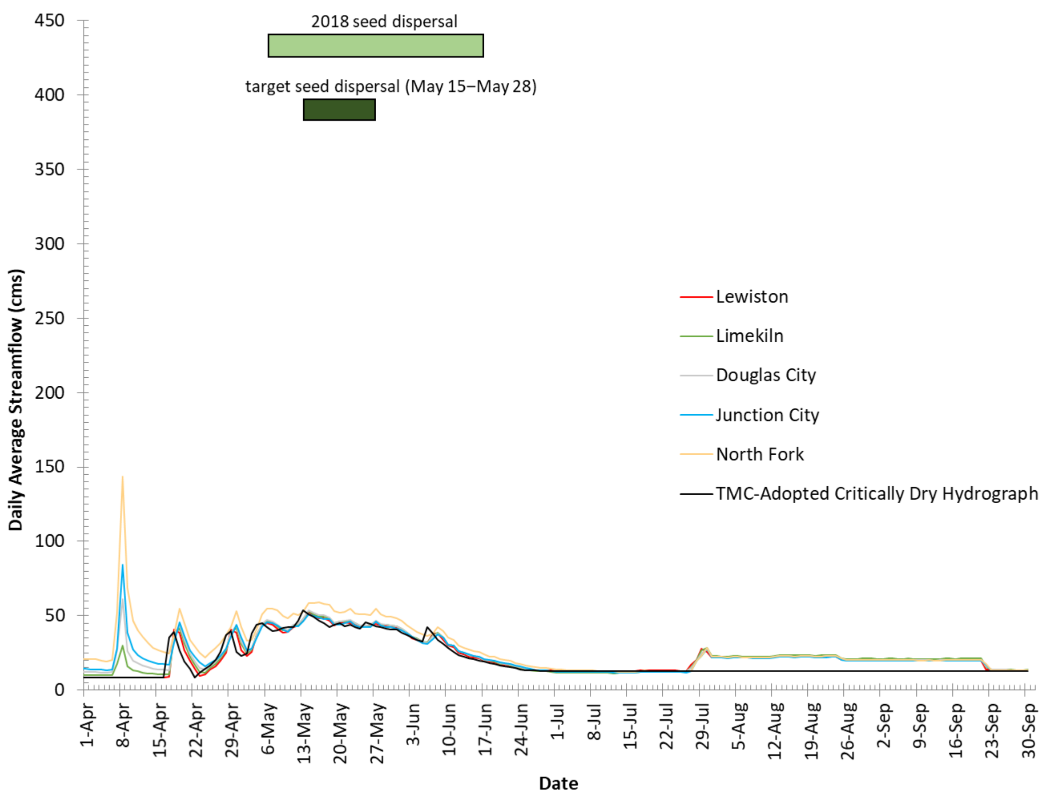

Figure 17. Annual WY 2018 hydrograph at five streamflow gages, with 2018 seed dispersal and recommended target seed dispersal periods overlaid.

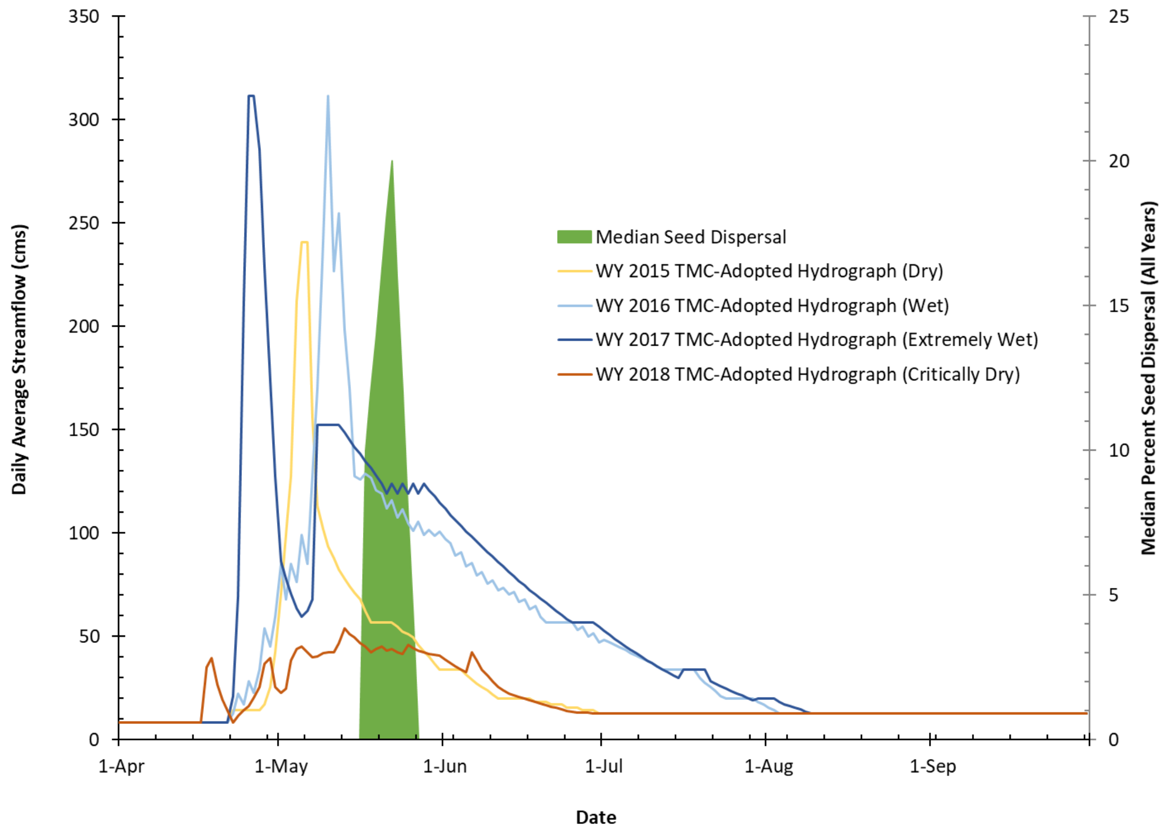

Figure 18. Median seed dispersal period for all years combined overlaid onto the Trinity Management Council (TMC) approved hydrographs for WY 2015 through WY 2018.

5.4 Developing a Predictive Model

In addition to having a shorter target seed dispersal period, it would be useful during annual flow release planning to have a model that could predict when seed dispersal might occur based on known factors such as Julian date, accumulated degree-hours, or some other factor(s). We investigated the possibility of developing a predictive model of when seed dispersal was likely to be highest. For our model selection using the AIC method, we included Julian date, and accumulated degree-hours as predictor variables, along with Julian date with a quadratic effect, and interactive terms between Julian date and accumulated degree-hours. We did not include site, tree, and year as variables because site and tree were not significant according to the Kruskal-Wallis test (Section 5.1) and it is likely that the significance of year was caused by an unknown variable associated with year (i.e., previous year water year class) and would introduce uncertainty to the model. The final model selected by the AIC method included all the input variables (Model 1).

Model 1: $\hat{P} = -395.60 + 0.14A + 4.89J - 0.01J^2 - 0.002AJ + 0.00005AJ^2$

Where:

$\hat{P}$ = predicted probability of seed dispersal,

A = accumulated hour, and

J = Julian date.

A goodness of fit test was conducted on the final model to determine if the model did a good job of explaining the probability of seed dispersal occurring. The null hypothesis in goodness of fit testing is that the data behave as the model predicts (i.e., the predictor variables selected in the model do have an effect on the probability of seed dispersal). The residual deviance of the model is used to test whether the null hypothesis is true. A p-value ≤ 0.05 would indicate a significant lack of evidence to support the null hypothesis (i.e., the model is not a good fit). In this case, our p-value was 1.0, indicating that our model fit the data well.

The relationship between the predictor variables was explored for collinearity. A correlation test was conducted and, as expected, Julian date and accumulated degree-hours were highly correlated ($p< 0.05$) and can be seen when plotted against each other (Figure 19). However, we chose to keep both Julian date and accumulated degree-hours as predictor variables in the model because accumulated degree-hours can vary from year to year on a given Julian date. We wanted to keep that slight variation in the model since it can influence the probability of seed dispersal. In addition, collinearity between variables does not reduce a model's predictive power; it can, however, make it difficult to determine the effect of each predictor.

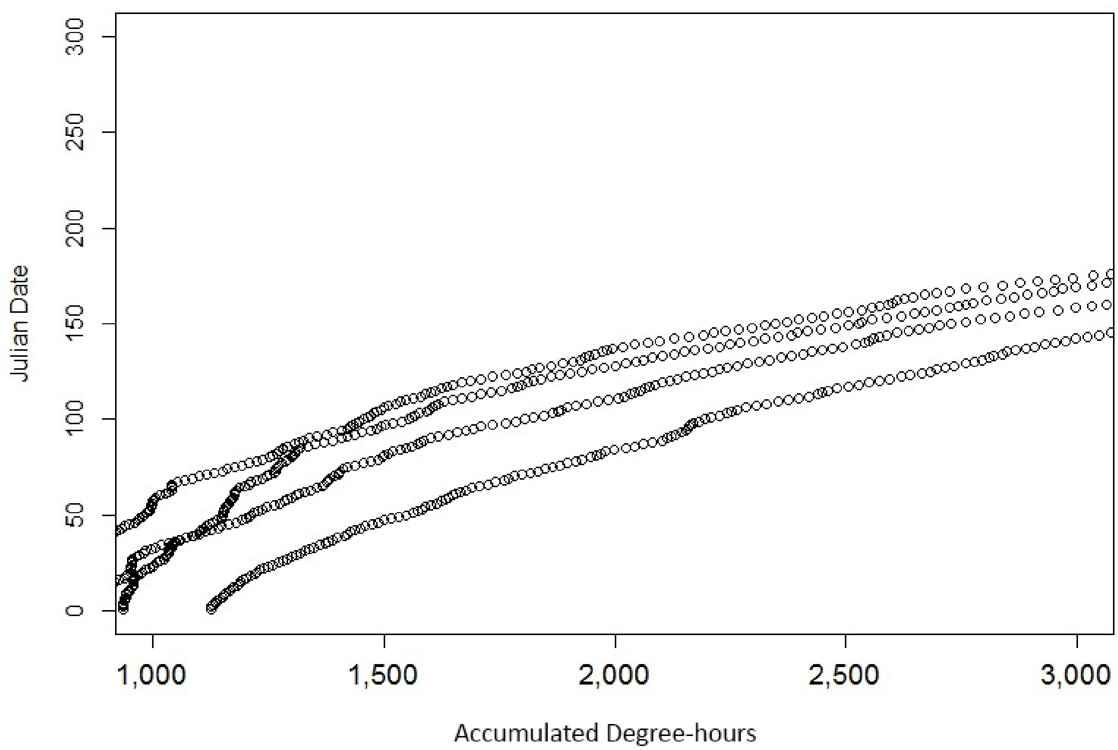

Figure 19. Julian date plotted against accumulated degree-hours for WY 2015–2018. The linear orientation of the points indicate that Julian date and accumulated degree-hours are highly correlated.

We wanted to test whether a predictive model could be developed with the current data such that a combination of Julian date and accumulated degree-hours could be used to predict the dates when seed dispersal would occur. To do this, the predict function in R was used to calculate probabilities of seed dispersal for Model 1 using a range of Julian dates (0–300) for five different accumulated hour values: 1,500, 1,750, 2,000, 2,250, and 2,500 accumulated degree-hours. The accumulated hour values were selected because they bracket the 2,000 accumulated degree-hours demarcation seen in Figure 10. The purpose of keeping accumulated degree-hour values constant for the analysis (instead of increasing as would typically occur), was to observe how seed dispersal probabilities and timing would differ between cooler years and warmer years. As accumulated hour values decreased, the highest probability of seed dispersal increased (0.99 for the 1,500 accumulated hour curve to 0.72 for the 2,500 accumulated hour curve) and occurred at later Julian dates (Figure 20, Table 8). The model suggested that seed dispersal occurs earlier in warmer years but at a lower probability. The probability of seed dispersal on Julian date 139 (May 19) is 0.72, regardless of the accumulated hour value on that date. May 19 is within the target seed dispersal period recommended in Section 5.3, which according to the Model 1, will capture the highest probability of seed dispersal in hotter years and increasing (though not the highest) probabilities of seed dispersal in cooler years (Figure 20).

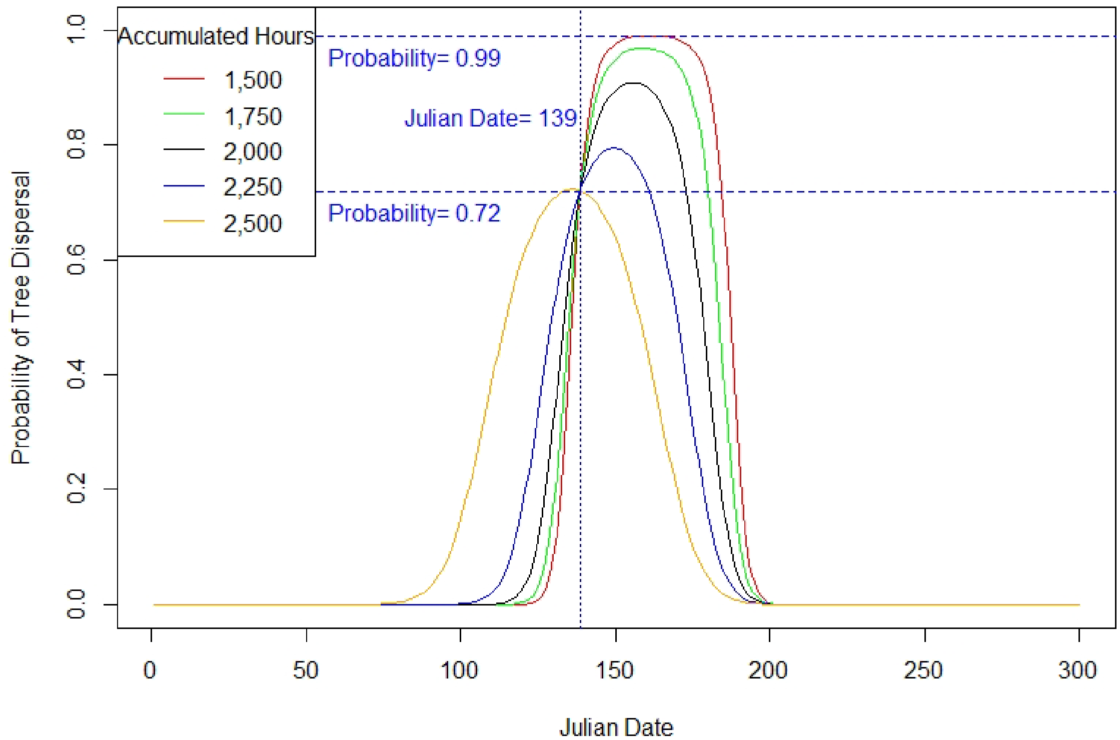

Figure 20. Probabilities of seed dispersal calculated using Model 1 for a range of Julian dates (0–300) under five different accumulated hour scenarios: 1,500, 1,750, 2,000, 2,250, and 2,500. All scenarios overlapped at Julian date 139 (May 19), when the probability of seed dispersal was 72%.

Table 8. The highest probability of dispersal and the range of Julian days and associated calendar date when the peak occurred for each accumulated hour input scenario calculated from Model 1.

Accumulated Degree-hours	Highest Probability of Dispersal	Range of Julian Days	Associated Calendar Date*
1,500	0.99	154–169	June 3–18
1,750	0.97	155–163	June 4–12
2,000	0.91	153–159	June 2–8
2,250	0.79	146–154	May 26–June 3
2,500	0.72	132–140	May 12–20

*For a normal calendar year (non-leap year).

6 DISCUSSION AND RECOMMENDATIONS

The seed dispersal data analyzed in this synthesis report represent the natural variation in seed dispersal timing observed within the Project Reach. The estimates of seed dispersal timing were based on four years of observation data. Additional data may or may not improve the estimate of seed dispersal timing in the Project Reach; however, additional seed dispersal monitoring should be continued because monitoring has not occurred in all water year types, and four years of data may not encompass all the variation present in seed dispersal timing.

Seed dispersal timing occurs over a relatively consistent length of time and similar period within a year, but the start and end dates can shift by at least one month between years. Local and regional changing climate conditions may affect seed dispersal timing, which is important to document if we want to be able to adapt to climate change. Numerous studies have shown that the timing of many plants' life histories has shifted to occur earlier in the year in response to increased air temperatures associated with climate change (Osborne et al. 2000, Chmielewski and Rötzer 2001, Cleland et al. 2007). In fact, a shift to earlier timing is one of the most sensitive plant responses to warming trends (Wolkovich et al. 2012). We do not know whether our seed dispersal monitoring data reflect black cottonwood's response to changing air temperatures. However, WY 2015 was the warmest year on record globally, and the four warmest years on record have occurred since 2010 (NOAA National Centers for Environmental Information 2016). Therefore, it is likely that cottonwood seed dispersal timing is currently adjusting to new global and regional temperatures. The amount of adjustment is unknown; relying on the current target seed dispersal period without additional monitoring data could lead to inaccurate flow release timing if seed dispersal continues to occur earlier. Continuing to monitor seed dispersal timing will inform future flow release planning, increase management flexibility in response to increasing temperatures resulting from climate change, and improve our understanding of black cottonwood life history.

The power analysis suggested that at least 11 years of data would be needed to detect differences between trees, if they exist. Although our results to date support the idea that there is a consistent portion of the black cottonwood seed dispersal period year to year, four years of data are likely not adequate to characterize the system. A single additional year of monitoring data (for a total of five years) would improve the power of our data analyses. The power analysis also suggested that additional trees would be needed to improve our ability to detect differences between localized sites; however, if the entire Project Reach is treated as the site, our sample size of 39 trees is adequate to detect statistically significant differences if they exist.

- **Recommendation #1:** Seed dispersal monitoring should be continued through at least 2019, but ideally until at least 11 years of data have been collected.

The prior year water year class may affect the timing of seed dispersal the following year. The induction of flowering has been well studied, but factors that encourage seed dispersal are less well understood. Early season temperature conditions may influence the timing of seed dispersal (Stella et al. 2006, Wolkovich et al. 2012, Schröder et al. 2014). Black cottonwood produces next year's flower buds during the current year's growing season (Boes and Strauss 1994, Kaul 1994). What's more, the early-flowering plants in a population are usually always the first to flower, and the late-flowering plants usually flower later, meaning there may be inherent differences between individuals in a population (i.e., differences between trees, Boes and Strauss 1994). Flowering begins in response to environmental cues and genetic predisposition (Kim et al. 2009, Amasino and Michaels 2010). The target seed dispersal period developed in this synthesis report accommodates the early seeders in warmer years and the late seeders in cooler years, based on the four years of data. Without multiple years of each water year class, however, it is not possible to know whether the preceding year's water year class influences the timing of seed dispersal the following year.

- **Recommendation #2**: (Modification of Recommendation #1) Continue seed dispersal monitoring until three years of each water year class have be monitored. This would yield at least 15 years of data, thus meeting the increased sample size requirement suggested by the power analysis.

The target seed dispersal period, May 15–28, narrows the broad seed dispersal window to simplify annual flow planning and should improve the germination and establishment of black cottonwoods on upper bars and floodplains. The predictive model developed during this synthesis report suggests that on calendar day May 19, the probability of seed dispersal is 72%. And unless the year is uncommonly warm (i.e., accumulated degree-hours exceed 2,500 by May 19), the probability of seed dispersal will increase after May 19. Annual flow planning in WY 2019 used the target seed dispersal period, and anecdotal evidence showed that seed dispersal was occurring within this period and during scheduled flow recession. To further test the predictive ability of Model 1, annual flow planning in WY 2020 could use May 19 as the day around which to schedule the receding limb at a recession rate that supports seedling root growth (i.e., 3 cm/day). This approach should be coupled with phenological observations and modified if field conditions suggest that May 19 is not appropriate.

- **Recommendation #3:** Assess the need for a better predictive model in relation to Program objectives by using it for WY 2020 annual flow planning and comparing the predicted date of highest median seed dispersal with the actual date of highest median seed dispersal observed in WY 2020.

Model 1 included two potential causal factors influencing the timing of seed dispersal: photoperiod and air temperature. We used Julian date as a proxy for photoperiod and accumulated degree-hours as a proxy for air temperature. Photoperiod is a primary factor that influences flowering timing, and all plants respond to it in some way. Photoperiod (i.e., day length) has been shown to influence the timing of developmental stages in plants (Taiz et al. 2015). Total day length for calendar years 2010–2015 was downloaded from the U.S. Naval Observatory website (https://aa.usno.navy.mil/data/docs/Dur_OneYear.php). There was no significant difference in day length between the six years based on a single-factor ANOVA (F=0.001, p=0.999). Therefore, photoperiod would not account for seed dispersal differences between years. However, some as yet unknown intrinsic attribute to the daily number of hours of sunlight (or darkness) must at least partially influence when black cottonwood disperses its seeds.

Because day-length increases with Julian date during the seed dispersal period, and the longer days accumulate degree-hours faster, Julian date and accumulated degree-hours are auto-correlated. The collinearity between the variables was not accounted for in the GLM developed to predict when seed dispersal is likely to occur. Julian date and photoperiod were simple predictors used to forecast the timing of seed dispersal; however, more explicit variables contributing to the relationship between Julian date and accumulated degree-hours could be used instead. For instance, solar radiation may vary at each site, or even at each tree. Trees exposed to sun all day would be expected to accumulate heat faster than trees located in a valley wall shadow for half the day. Similarly, relative humidity, access to groundwater, soil moisture, minimum and maximum local air temperature, wind speed, and local precipitation could be potential factors influencing the timing of capsule development and subsequent seed dispersal. Assessing relationships between these variables and seed dispersal timing could improve the predictive ability of the model developed as part of a future extension of this study. However, local environmental factors at each monitoring site have not been monitored and therefore site-specific data are not currently available.

Additionally, a robust predictive model that includes the specific factors that influence seed dispersal timing could theoretically predict the best time to release peak spring flows coincident with the highest probability of seed dispersal. A predictive model like this, if accurate, could reduce a lot of the uncertainty associated with flow release timing. Additionally, it may improve the annual flow release planning process by adding a unique filter to the target seed dispersal period (i.e., it could make annual predictions more accurate based on the predictors chosen for the model, such as previous water year type or local air temperatures). The model developed during this synthesis report begins to get at predictive relationships, but shortcomings in the available environmental data limit its predictive capability.

- **Recommendation #4:** Additional phenology monitoring coupled with local environmental monitoring should be conducted to assess the predictive ability of the model and simultaneously collect data to improve the predictive model. Use of HOBO sensors to monitor local air temperature, humidity, precipitation, wind speed, light intensity, and/or soil moisture at each seed dispersal monitoring site may identify the most important factors influencing the timing of black cottonwood seed dispersal in the Project Reach.
- **Recommendation #5:** Solar radiation analysis could be conducted to determine if there are site-level or tree-level differences in the amount of sunlight, and therefore potentially heat, that each tree receives.
- **Recommendation #6**: Run an n-mixture model analysis to account for the lack of independence between observations within a year (each tree was sampled weekly, therefore were not independent observations).
- **Recommendation #7:** Update the new n-mixture GLM using new monitoring data.
- **Recommendation #8:** Develop a temperature model to be used with the GLM to help water resource managers predict seed dispersal periods and when to release water. The predicted daily accumulated degree-hours can be plugged into Model 1 equation to calculate a daily probability of seed dispersal and water resource managers could release water on a day when a probability threshold (e.g., 0.72) is met.

Vernalization is another environmental cue to which many plants respond (Kim et al. 2009, Amasino and Michaels 2010). Vernalization is a prolonged exposure to cold temperatures that enables plants to flower when conditions improve in the spring (Kim et al. 2009). Timing of flowering is partially regulated via protein production, which is genetically regulated (Amasino and Michaels 2010). The proteins stimulate physiological responses to increasing temperatures and longer day lengths. Protein synthesis is temperature sensitive; therefore, air temperatures, both warmer and cooler, influence the timing of bud release annually. Some proteins are stabilized by light and therefore photoperiod can play an important role (Amasino and Michaels 2010). The effects of vernalization were not investigated during this synthesis report but could prove to be important to the timing of flower induction and ultimately seed dispersal.

- **Recommendation #9**: Include accumulation of cold hours, similar to accumulated heat hours, in the next iteration of seed dispersal timing analysis.

In black cottonwood, establishment of a particular cohort is typically episodic following higher flood events; widespread establishment does not occur every year, despite copious seed production (Auble and Scott 1998, Mahoney and Rood 1998, Rood et al. 1998). WY 2017 was Extremely Wet and 339.8 cms (12,000 cfs) was released from Lewiston during the spring ROD release. This is the largest flow to be released since implementation of the ROD. WY 2017 flow releases provided an ideal opportunity to assess whether management actions have successfully achieved the goal of promoting black cottonwood on upper bars and floodplains. Specifically, were higher streamflows able to create suitable seed beds upon which black cottonwood seeds could germinate, and was the receding limb sufficiently slow to allow germinating seedlings' roots to grow down with the receding groundwater?

- **Recommendation #10:** Recruitment surveys scheduled as part of the WY 2019 riparian monitoring should identify seedbed locations created by the 2017 flows and quantify the number of black cottonwood seedlings.

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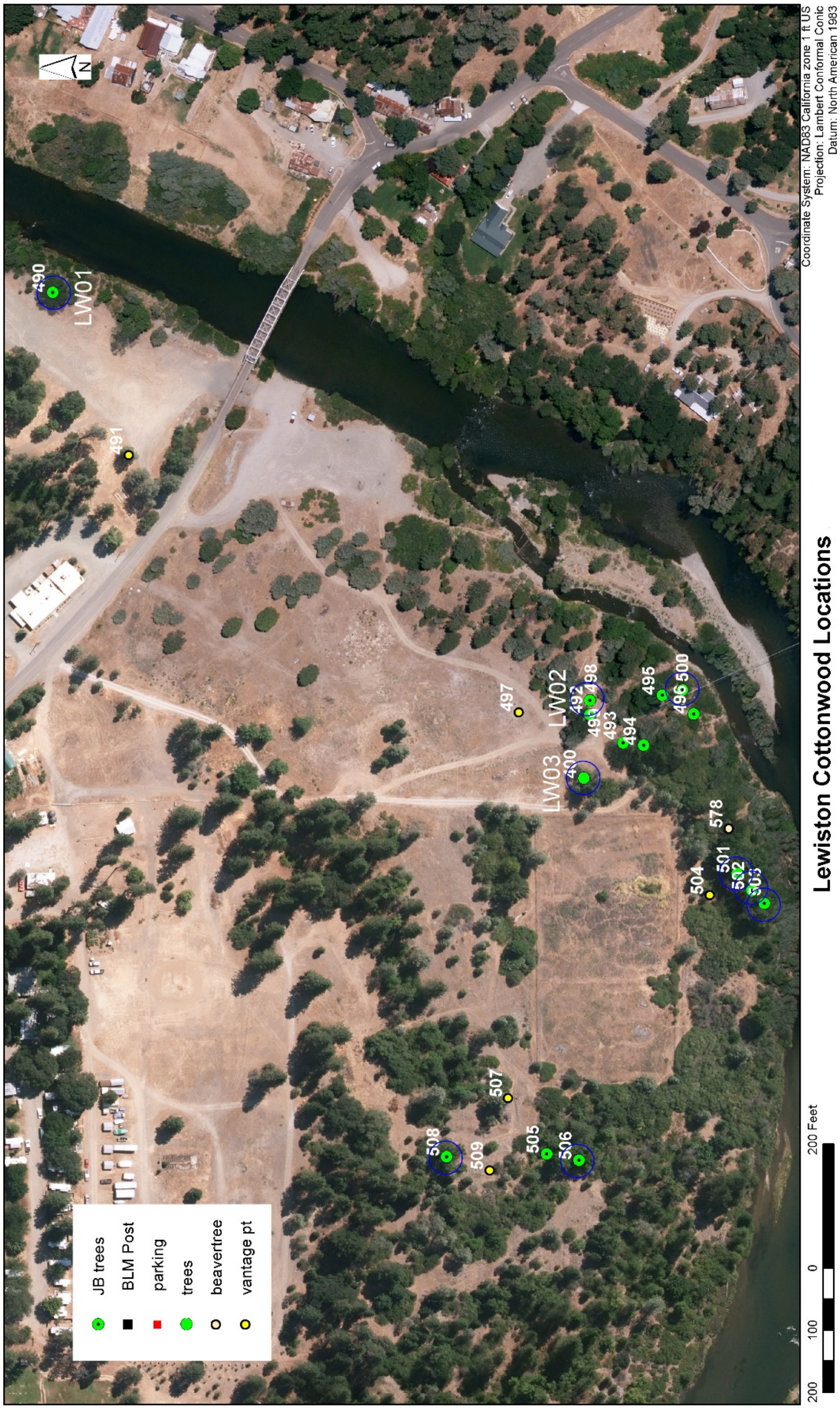
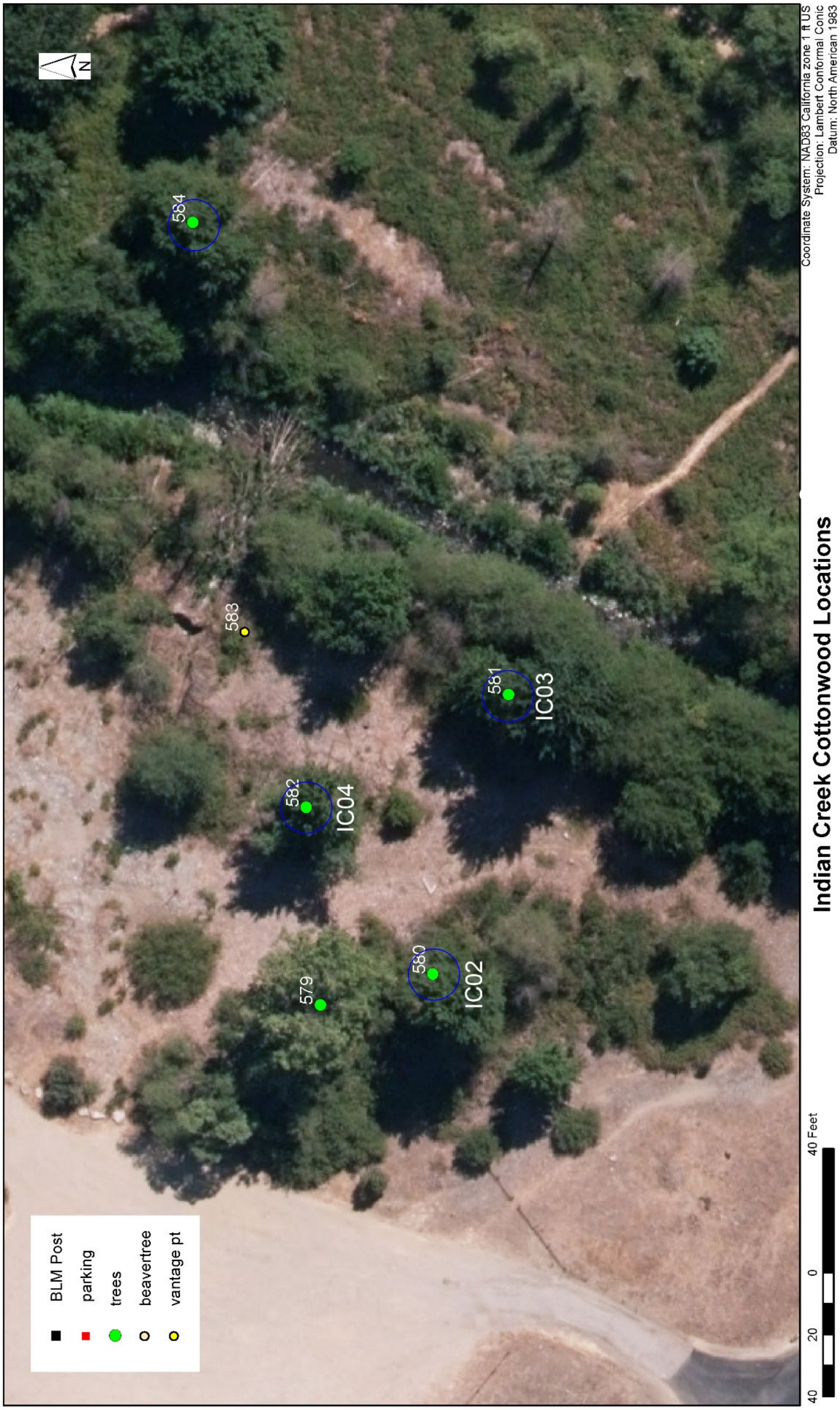
8 APPENDIX A: TREE LOCATIONS 2015–2018



Lowden Ranch Cottonwood Locations

Coordinate System: NAD83 California zone 1 ft US
Projection: Lambert Conformal Conic
Datum: North American 1983



Indian Creek Cottonwood Locations

60 30 0 60 Feet

Coordinate System: NAD83 California zone 1 ft US
Projection: Lambert Conformal Conic
Datum: North American 1983

Douglas City (A) Cottonwood Locations


Coordinate System: NAD83 California zone 1 ft US
Projection: Lambert Conformal Conic
Datum: North American 1983
Junction City Cottonwood Locations
JC01
JC02
JC03
JC04
JC05
JC06
JC07
JC08
JC09
JC10
Cottonwoods
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0
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200 Feet

9 APPENDIX B: 2018 WORK PLAN

I. PROPOSAL NARRATIVE

COMPONENT 1. PROJECT ID CODE:

COMPONENT 2. TITLE

Quantification of Cottonwood Seed Dispersal Period Synthesis Report Proposal

COMPONENT 3. PRINICIPAL INVESTIGATOR(S)

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COMPONENT 4. PARTNERSHIPS AND ROLES

None.

COMPONENT 5. STATUS OF PRIOR YEARS' FINAL REPORTS AND DATA DELIVERABLES

Cottonwood phenology monitoring was conducted in WYs 2004, 2015, and 2016. Cottonwood phenology monitoring is ongoing during WY 2017. WY 2004 surveys used a unique protocol, and WY 2015-2017 surveys used the same protocol where the same thirty individual trees were monitored at five sites from Lewiston to Junction City. Data analysis of WY 2016 is currently in progress, and results will be reported and delivered to the TRRP Data Steward in the annual riparian monitoring report by June 30, 2017. Data analysis and reporting will be conducted through the remainder of WY 2017 and be delivered to the TRRP Data Steward in the annual riparian monitoring report by June 30, 2018. The WY 2004 survey was summarized in HVT and M&T 2006 and the WY 2015 survey was reported in HVT and M&T 2016. Data analysis of WY 2016 is currently in progress, and results will be reported and delivered to the TRRP Data Steward in the annual riparian monitoring report by June 30, 2017. Data analysis and reporting will be conducted through the remainder of WY 2017 and be delivered to the TRRP Data Steward in the annual riparian monitoring report by June 30, 2018.

COMPONENT 6. PROBLEM DESCRIPTION

Cottonwood recruitment on upper bars and floodplains is a stated goal of the IAP (TRRP and ESSA Technologies Ltd 2009), and the TRRP has made considerable effort since 2006 to create a hydrograph that promotes cottonwood recruitment. Flow benches, or periods of steady flow, have been added to the receding limb of the hydrograph and are intended to coincide with the cottonwood seed dispersal period. In the 64-km Project Reach of the Trinity River (from Lewiston Dam down to the North Fork Trinity River), seed dispersal timing was measured in 2004, and this window was assumed to accurately reflect cottonwood seed dispersal during most years. Field observations and peer-reviewed publications (e.g., Stella et al. 2006) since 2004 have suggested that cottonwood seed dispersal may vary annually depending on weather conditions. Water year type, air temperature, groundwater availability, and individual tree variability of seed dispersal timing were hypothesized explanations for observed results. This proposal will statistically compare seed dispersal timing data from all years that data have been collected (2004, 2015, 2016, and 2017) to evaluate if they are significantly different from each other. Collected data will be used to develop a mean, median, and 95% confidence interval around the average seed dispersal timing, to reduce uncertainty about cottonwood seed dispersal timing and, if the results are appropriate, provide a consistent seed dispersal window to be targeted regardless of water year type.

COMPONENT 7. INTEGRATED ADAPTIVE PLAN (IAP) OBJECTIVES LINKAGES

The data or results directly address or could be used to support the evaluations of the following IAP Sub-Objectives (TRRP and ESSA Technologies 2009):

Sub objective 5.1: Promote diverse native riparian vegetation on different geomorphic surfaces that contributes to complex channel morphology and high quality aquatic and terrestrial habitat

5.1.1 Increase species, structural, and age diversity of riparian vegetation to improve and maintain wildlife habitat

5.1.2 Encourage establishment of riparian species on surfaces within the future channel migration corridor that will recruit LWD

5.1.3 Encourage establishment of vegetation that provides habitat for anadromous fish, aquatic organisms and aquatic/riparian wildlife

COMPONENT 8. PROJECT IMPLICATION(S)

Black cottonwood recruitment is an important Programmatic objective for normal and wetter water years, and this objective provides an ecological basis for timing and ramping down spring flows. In order to achieve black cottonwood recruitment, targeted surfaces must be moist during the seed dispersal period. There are four years of data on the timing of cottonwood seed dispersal (HVT and M&T 2006, HVT and M&T 2016, HVT and M&T *in review*, and one monitoring effort that was ongoing during the development of this proposal) yet hydrograph planning relies on a single year's data (2004; HVT and M&T 2006). This proposal would synthesize all four years of data to produce a cottonwood seed dispersal timing model that can be applied for all water years wetter than critically dry, with measures of uncertainty around the predicted beginning and end dates. Without this synthesis, the monitoring that has already been conducted would not be available in an adaptive management capacity. Hydrograph planning is expected to be simplified; and assessment of causal factors responsible for hydrograph success or failure will likewise be simplified, in that the timing of black cottonwood seed dispersal will be much better understood as an outcome of the work described in this proposal.

COMPONENT 9. OBJECTIVES

The objective of this proposed work is to synthesize existing data to quantify the seed dispersal period for black cottonwood within the Project Reach that can consistently be applied during annual flow scheduling so that the timing of key flow benches (e.g., 169.9 cms) can coincide with cottonwood seed release.

COMPONENT 10. METHODS.

Cottonwood seed dispersal was studied at Lower Junction City in 2004 and involved counting the seeds collected on seed traps and visual estimates of flowering, fruiting, and seed dispersal. Seed dispersal monitoring data were summarized to yield the existing black cottonwood seed dispersal period; however; data analysis was not formally reported or submitted to the TRRP. Additional cottonwood phenology data were collected in 2015 at five study sites (Lewiston, Douglas City, and Junction City). Data collection in 2015 included identification and geolocation of dominant females, and documenting at each tree the percentage of canopy covered with catkins expressing dehisced capsules, and documenting tree height, tree diameter at breast height, and increment cores to characterize the age, size, and growth rate of trees. The five study sites were visited weekly between March 30 and June 30, 2015. Analyzed data were reported in the Water Year 2015 report (HVT and MA 2016), which was delivered to TRRP along with associated data on September 14, 2016.

All black cottonwood phenology data will be compiled then converted into the same format to allow comparison across all years. In 2004, phenology observations included visual estimations of flowering, fruiting, and seed release using Daubenmire cover classes (1=0–5% cover, 2=6–25%, 3=26–50%, 4=51–75%, 5=76–95%, 6=96–100%). Starting in 2015 and repeated in 2016 and 2017, phenology observations included flowering, fruiting, and seed release in the upper third, middle third, and lower third of each tree canopy using a continuous cover scale (0–100%). To enable comparisons between 2004 and 2015–2017 data, the observed measurements must be converted to the same scale. Therefore, all observations from 2015–2017 will be averaged for each tree and then converted to Daubenmire cover classes, and the midpoint of each cover class will be used for all measurements (2004, 2015–2017). For instance, if a tree in 2015 had an average of 65% of the canopy releasing seeds, it would be converted to Daubenmire cover class 4 (51–75%). To allow statistical analysis, the cover class 4 would be assigned 62.5% cover, the midpoint between 51% and 57%. Similarly, a tree from 2004 with average percent canopy releasing seeds in Daubenmire class 2 would be assigned 37.5% cover.

Several comparisons of existing black cottonwood phenology data will be made (by existing, we include 2004, 2015, 2016, and 2017 observations, even though 2017 observations have not yet been made, because they will be made by the time the proposed work is conducted). Annual comparisons of seed dispersal timing, which will have been reported separately in WY 2015, WY 2016, and WY 2017 Annual Monitoring Reports, will be summarized again. Additionally, more detailed analysis of seed dispersal in different portions of the tree canopy will be conducted. An index of seed density will be calculated by summing the three estimates of the percentage of canopy covered with catkins expressing dehisced capsules per tree (upper third, middle third, and lower third) for a given observation. It is expected that more fruits (i.e., capsules in catkins) will develop in the middle and upper third of each tree canopy.

Comparisons will also be made for 2015–2017 data when measurements were compatible. For these three years, analysis of variance (ANOVA) will be used to explore statistical relationships. Specifically, within-tree variation will be compared to between-tree variation, and within-site variation will be compared to between-site variation. ANOVA will be run on data from each year separately, and then run for all years. These results are expected to corroborate the results from the 4-year comparison.

Results from ANOVA are expected to show that there is wide variation in seed dispersal timing within individual trees but little variation between sites, suggesting that the seed dispersal timing period is stable across years. This expectation is based on results from 2004 and 2015 data, which have already been analyzed. The stable seed dispersal period will be defined by the average start date (10% of population releasing seeds), peak date (50%), and end date (90%), and be bracketed by the 95% confidence interval. If a stable black cottonwood seed dispersal period is defined, it will be overlaid onto the TMC-approved hydrographs from all water years that were designed to promote black cottonwood recruitment as well as the WY 2004 and WY 2015 hydrographs. The defined seed dispersal period will also be compared to the previous estimates contained in the Trinity River Flow Evaluation Final Report (USFWS and HVT, 1999) with a discussion of flow management implications if the timing has shifted. The timing of the recession limb and associated flow benches from at least two water year types (Dry and Wet) will be compared with the start, peak, and end of seed dispersal to ensure the stable seed dispersal period encompasses the range of ROD flows likely to occur.

The defined seed dispersal period will also be used as a focal point for a discussion of flow management considerations related to seed dispersal timing, e.g., the 21-day flow bench to maintain moist floodplain soils for seed germination before the end of the seed dispersal period.

If the analysis indicates that the seed dispersal period varies inter-annually at the population level, then this suggests that weather-related covariates (e.g., patterns of degree-day accumulation, solar insolation, precipitation patterns, and groundwater availability) may drive patterns of black cottonwood seed dispersal and would trigger a multi-variate modeling effort to predict the seed dispersal period. This modeling effort would be proposed after this proposed synthesis is completed.

COMPONENT 11. STUDY AREA

The Project Reach extends 64 km from Lewiston Dam to the confluence with the North Fork Trinity River. Specific study sites are located at Lower Junction City, Douglas City near Weaver Creek, Douglas City near Indian Creek, Lowden Ranch, and Lewiston (near the Old Bridge).

COMPONENT 12. PROJECT DURATION AND TIMELINE

Data compilation and analysis will occur following funding implementation in FY 2018. Because all data are currently stored in the same location, compilation is not expected to take long. Similarly, because black cottonwood phenology has been monitored for three years in a row, summary data for each year are already prepared, and data analysis comparing results between years is not expected to be a lengthy process. All synthesis, including reporting, will be completed by the end of 2018.

Action	FY 2018			
	1st Q	2nd Q	3rd Q	4th Q
Data Synthesis		X		
Annual Report	X			
Final Synthesis Report			X	
Data Delivery				X

Q = Quarter in year

COMPONENT 13. PRIORITY

Although there is no legal mandate to synthesize black cottonwood seed dispersal periods, it is a high priority to develop a stable model of seed dispersal timing for use in hydrograph planning. Considerable effort has already been made to collect black cottonwood phenology data. Synthesis of those data is integral to cost-effective adaptive management, will reduce uncertainty during the hydrograph planning process, and will contribute to scientific knowledge of black cottonwood ecology.

COMPONENT 14. PRODUCTS AND DELIVERABLE SCHEDULE

November 15, 2017	Annual Report including a description of the current work status, and project schedule will be updated if needed. The annual report will be delivered in .doc format.
June 30, 2018	Final Synthesis Report delivered to TRRP in .doc and .pdf formats
July 31, 2018	Data Package delivered to TRRP in .xls and shapefiles

II. BUDGET

See attached budget spreadsheet. The total budget for the project is $32,602. The proposed work has been divided into the following tasks:

Task 1: Seed dispersal synthesis analysis

Task 2: Synthesis report

Task 3: Annual reporting

Task 4: Data delivery

Task 5: Project management