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Hydration as a possible colonization cue: Rain may promote seed release from black cottonwood trees

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ABSTRACT

Within the Salicaceae, the poplar trees and willow shrubs display an *r*-selection reproductive strategy, with the production of vast numbers of seeds but these are tiny, viability lasts only a few weeks, and very few seedlings establish and mature to contribute to the woodland populations. The timing of seed release is consequently critical and for cottonwoods, riparian poplars, seed release has been reported to follow the spring peak in river flow. To investigate the prospective coordination between environmental conditions and seed release we undertook daily observations of black cottonwoods (*Populus trichocarpa*) over four summers along the lower Duncan River in southeastern British Columbia, Canada. Seed release involved a sequence of pulses with the first after about 400 cumulative degree days (base 5 °C) in the growth season. There were four or five pulses annually with each extending one to six days and occurring through June and July and unexpectedly, into early August. The pulses of seed release were not coordinated with changes in river flow but all 18 pulses over the four years followed rain events. We thus conclude that in a humid climate mountain ecoregion, rain and possibly post-rain warming may provide environmental cues that trigger cottonwood seed release. This hygrisence could retain the near-mature seeds on the maternal tree, prolonging their viability, and their release after rain would provide moist substrates, benefitting seedling establishment. We further conclude that in a humid ecoregion, the river flow pattern would be less important for riparian seedling colonization than in semi-arid regions, where summer rain is sparse. In all ecoregions, occasional high river flows are essential for the fluvial geomorphic disturbance that creates the barren seedling colonization sites, and also to exclude flood-intolerant upland vegetation from encroaching into the riparian recruitment zones.

1. Introduction

Floodplain forests provide exceptionally rich habitats for birds and other wildlife, favored areas for human use, and contribute other ecosystem services including river bank stabilization, interception and assimilation of nutrients and other water contaminants, and the provision of leaf litter and woody debris that contribute to the aquatic food-web (Naiman et al., 2010). Around the Northern Hemisphere these important and biodiverse riparian woodlands include cottonwoods, riparian-adapted poplar (*Populus* sp.) trees, as the primary colonizers of barren areas that are formed with the scour and deposition of the alluvial sands and gravels (Karrenberg et al., 2002; Rood et al., 2003; Cooke and Rood, 2007). The cottonwood trees subsequently mature to provide keystone species for the riparian woodland ecosystems (Naiman et al., 2010).

Cottonwoods are ecological specialists with life history and ecophysiological traits that are adapted to the physically-dynamic floodplain zones (Karrenberg et al., 2002; Rood et al., 2003). These trees display an *r*-selection reproductive strategy, as they produce vast numbers of tiny seeds but very few germinate and far fewer survive to contribute mature trees to the woodland population. The tiny seeds are reportedly released through a limited interval in late spring and early summer, and are viable for a few weeks if dry or only a few days if moistened (Fenner et al., 1984; Dixon, 2003); there is thus no year-round seed bank. With this restricted interval of seed dispersal and viability, the timing of seed release becomes critical (Guilloy-Froget et al., 2002; Stella et al., 2006).

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Table 1
Prior reports of the pattern of cottonwood seed release. R. = River and abbreviations of American states or Canadian provinces are indicated.

Source	Species	Location	Method	Sampling interval	Release pattern	Release duration[a]
Farmer (1966)	*Populus deltoides*	Lower Mississippi R., MS	Observations of seed dispersal by specific trees	Weekly	Progressive	13 wks, mid-May to late Aug
Fenner et al. (1984)	*P. fremontii*	Salt R., AZ	Water bucket seed traps	Weekly	Single peak with tail	9 wks, mid-Apr to mid-June
Virginello et al. (1991)	*P. angustifolia*	Oldman R., AB	Quadrats along banks	Weekly	Single peak	3 weeks, mid- to late June
D'Amico (1997)	*P. angustifolia*, *P. deltoides* & hybrids	Boulder Ck., CO	Small sticky traps	1 or 2 week intervals	Broad peak but limited results	5 wks, June to early July
Cooper et al. 1999	*P. fremontii*	Green and Yampa R., CO	Sticky seed traps	4–15 days	Single peak with tail	4 wks, late June to July
Guilloy-Froget et al. (2002)	*P. nigra*	Garonne R., France	Observations of marked branches	Weekly	Skewed peak or bimodal	8 – 13 wks, mid-May to mid-July
Stella et al. (2006)	*P. fremontii*	Tuolumne, CA	Observations of catkins on trees	~weekly	Bimodal or skewed single peak	12 wks, May through July
Meier (2008)	*P. trichocarpa*	Middle Fk. Flathead R., MT	Pans with water, and landowner observations	3–5 days	Skewed major peak with minor peak	6 wks., June into July
Gonzalez et al. (2010)	*P. alba*	Middle Elbro R., Spain	Sticky traps and observations	3–4 days	Major peak and minor peak	7 wks, April to May
Kehr et al. (2014)	*P. fremontii*	Verde R., AZ	Sieved seeds from water	Bi-weekly	Not determined	4 wks, April

[*] Additional reports of seed release duration but not patterns are provided by Guilloy-Froget et al. (2002) with values of 2–3 wks (3 reports), 3–6 wks (3), 8–9 wks (4) and 12 wks.

Especially in dry semi-arid ecoregions, seed dispersal and subsequent seedling colonization is apparently coordinated with the seasonal river flow pattern and often occurs during the river stage recession after the late spring peak (Table 1). The river recession progressively exposes saturated stream banks, providing favorable conditions for seed germination and seedling establishment and survival, which enable cottonwood colonization (Kalischuk et al., 2001; Karrenberg et al., 2002; Dixon, 2003). Particularly along regulated river reaches downstream from dams, cottonwood populations have been declining and this has often involved changes in the river flow regime and the subsequent failure of seedling recruitment, which is essential to compensate for the aging population (Rood et al., 2005; Tiedemann and Rood, 2015). Following from this environmental decline, Guilloy-Froget et al. (2002) and Stella et al. (2006) have stressed that successful conservation and restoration of cottonwood forests especially along regulated rivers will depend upon a better understanding of the phenology of seed release and its coordination with hydrometeorological conditions.

Guilloy-Froget et al. (2002) reviewed the literature related to the timing of cottonwood seed dispersal and emphasize the chronology relative to the typical seasonality of the stream flow regime. The various studies have extended from the Campbell, 1885 report of cottonwood seeding after the flood peak, and there have been many subsequent observations of the overlap in timing of cottonwood seed release and receding river flows (Farmer, 1966; Cooper et al., 1999). It has consequently been concluded that there would have been evolutionary selection for appropriate scheduling but the view has also been that the prospect for specific coordination in a particular year would be stochastic (Gonzalez et al., 2010) and as Stella et al. (2006) suggest, '*It is unlikely that elevated river flow directly triggers seed release in a given year*'. Stella et al. (2006) extend the analysis of seasonality and demonstrate that temperature is important and can delay or accelerate both the interval of seed release and the timing of the spring flow peak thus benefiting the hydroecological coordination. They subsequently found that analysis of the thermal sum with degree days improved the projection of the interval of cottonwood seed release over an estimate based on consistent seasonal timing across years.

While this consideration of temperature and seasonal coordination should improve the prediction of cottonwood seed phenology, there are still substantial uncertainties and even the basic seasonal pattern is poorly understood. As Guilloy-Froget et al. (2002) recognize, prior studies have applied different methodologies, complicating comparisons, and these have generally had a coarse time-step, being based on observations of trees or fallen seeds at weekly, bi-weekly or monthly intervals. We have been studying riparian cottonwoods along many rivers and it appeared that seed release could vary on a shorter time-scale, with substantial day-to-day variation. We thus undertook this study to track seed release on a daily basis over multiple summers. This analysis was part of a larger project to assess the possible changes to cottonwood seedling recruitment following a deliberate revision in the pattern of dam operation and downstream river flow regulation (Polzin et al., 2010).

Following from the prior research (Table 1) we anticipated that annually there would be a major interval of seed release that would be limited to a few weeks duration. Further, we expected that this would occur through a relatively similar seasonal interval across years, but would be slightly accelerated or delayed by warm or cool weather, respectively. This expectation was based on the view that the timing of seed release would reflect locally-adapted evolutionary selection for the optimal recruitment interval that would follow the typical timing for the late-spring peak in river flow, but with some refinement following the particular spring temperature regime.

2. Methods

2.1. Duncan River cottonwoods

The study involved the lower Duncan River, which provides the north-end inflow into Kootenay Lake in southeastern British Columbia, Canada. This river was dammed in 1967 with the first major project following the 1964 Columbia River Treaty between the United States and Canada. The Duncan Dam does not include a hydroelectric power plant and stores water for subsequent release downstream through a sequence of hydroelectric dams on the Kootenay River and downstream along the Columbia River. The lack of a hydroelectric facility allows additional flexibility in the operation of the Duncan Dam and following from this, BC Hydro recently implemented a new flow regime, 'Alt73'

(Alternative 73), that was intended for environmental benefit and particularly for floodplain forest reproduction and for the river and lake fishery (Polzin et al., 2010). Our study was part of the environmental monitoring intended to assess the consequence of the new environmental flow regime on riparian woodlands and especially the black cottonwoods, *Populus trichocarpa*, syn. *Populus balsamifera* subsp. *trichocarpa*, that provide the predominant riparian tree and the keystone species for the riparian woodlands.

For the assessment of the chronology of seed release along the lower Duncan River, downstream from the Duncan Dam, we observed the woodland canopy with daily observation from a fixed viewpoint above the woodland on an adjacent hill-slope above the Town of Argenta, near the outflow delta. There was also generally a drive through the woodland from Argenta upstream along the Duncan River to the Town of Meadow Creek, near the Duncan Dam. The extent of overall daily seed release from the cottonwoods was subsequently rated on a 4-point scale from 0 = no seeds, 1 = slight release, 2 = moderate release, to 3 = heavy release. Notes and photographs were taken to assist in coordinating the assessments. Observations commenced with the initial catkin flushing in April and extended through the period of flowering, seed development and release.

In the first study year, 2009, the observations emphasized June and July, the anticipated seed release interval. We also undertook seedling counts in quadrats along study transects (Polzin et al., 2010) and these revealed that there was some further seed release in August of 2009. This prompted extension of the daily observation interval from June through August in the subsequent study years of 2010, 2012 and 2013. Limited assessment was undertaken in 2011, as pre-planned with a staggered environmental assessment program for Alt73.

To investigate the possible coordination with environmental conditions, we obtained the daily discharges (*Q*) for the Water Survey of Canada hydrometric gauge, 'Duncan River Below Lardeau River (#08NH118)'. We obtained daily minimum, maximum and mean temperatures and daily precipitation from the 'Duncan Lake Dam' weather station near Meadow Creek (Latitude: 50.24°N; Longitude: −116.97°; Elevation 548.6 m above sea level) from the Environment Canada database. For temperature, the patterns across the three daily measures were closely coordinated and consequently we only present maximum daily temperatures. We next plotted the summer seasonal patterns for the variables: seed release, river *Q*, precipitation, and temperature. The plots revealed the apparent correspondence especially between seed release and rain events and for statistical assessment we considered this possible association in timing. For this, we first broke the summer study seasons into 3-day intervals. For each interval, we also considered whether there was any rain or any seed release and if so, that interval was extended for the duration of that rain or seed release event. This resulted in 61 time intervals over the four years (June through July in 2009; June through August in the other years) and for each we considered whether there was rain and whether there was seed release. Thus, for each time interval the consideration was 'yes' or 'no' for the two variables and this produced a 2×2 matrix and we applied a Contingency Table χ^2 (Chi^2) analysis (Snedecor and Cochran, 1967).

2.2. Observations of 'late seeders'

Our observations of mid- to late summer seed releases along the lower Duncan River prompted two further questions: (1) does late seeding by cottonwoods occur in other regions, and (2) if so, is the late seeding from particular trees or from specific branches or catkins on trees that release most seeds earlier. Subsequently, through the summer of 2014 we observed black cottonwoods along the Elk River, around our long-term study sites near Fernie, BC (Polzin and Rood, 2006) and cottonwoods along the Oldman River near our Lethbridge long-term study sites where four cottonwood species and their interspecific and intersectional hybrids occur (Gom and Rood, 1999). Similarly to the lower Duncan River, the follow-up studies involved observations from higher positions above the woodland canopies as well as from with ground-level observations. Additionally, linking the Elk and Oldman River study sites, Highway 3 provides a transect corridor over the Crowsnest Pass through the Rocky Mountains and this allowed us to periodically view zones with the sequential cottonwood species along that elevational transect (Kalischuk et al., 2001). We undertook 60 observer days along these rivers and especially sought trees that were releasing seeds in mid- to late July and into August.

3. Results

3.1. Duncan River cottonwoods

Male catkin bud flushing provides the first observable annual developmental event in cottonwoods (Gom and Rood, 1999) and along the lower Duncan River, this commenced in the first week of April (Fig. 1). The male and then female catkins emerged and pollination would occur while the leaves were flushing in mid- to late April (Fig. 1). The seeds developed and seed release was first observed 20 June 2009, 19 June 2010, 19 June 2012, and somewhat earlier in 2013, commencing 9 June (Fig. 1). Following from the analysis of Stella et al. (2006) we considered the coordination of the commencement of seed release with heat accumulation based on degree days. From these results, we conclude that the base temperature for black cottonwood seed development along the Duncan River would be well below the base *T* of 15 °C applied by Stella et al. (2006) for *Populus fremontii* along the Tuolumne River in California. A base *T* of 5 °C was more suitable and consistent with the analyses of Kalischuk et al. (2001) for multiple cottonwood species through our study region and with Berg et al. (2007) for black cottonwoods in southwestern Alberta. Thus, seed release along the Duncan River commenced after about 400 degree days with a base of 5 °C, and the earlier commencement in 2013 was associated with warmer weather in May and June that reached the same degree-day threshold as the commencement of seed release in the other study years (Fig. 1).

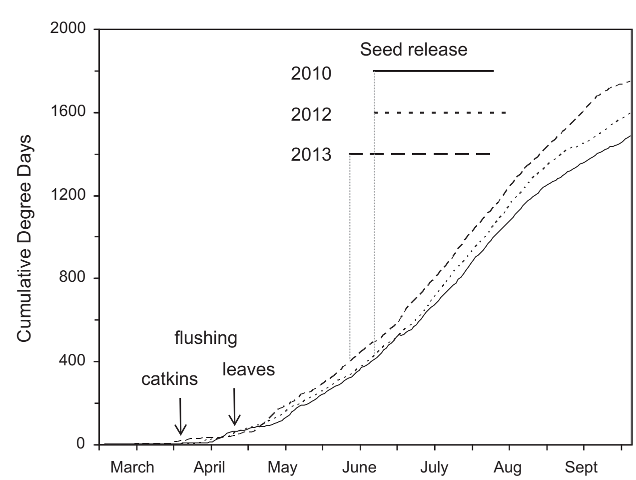

Fig. 1. Cumulative degree days above 5 °C at Meadow Creek near the lower Duncan River, British Columbia for three years and the intervals of cottonwood seed release. As indicated by the vertical and horizontal dotted lines, seed release commenced with ~400 DD_5 over the years.

The subsequent annual seed release included four or five release events that occurred in late June through July and into early August (Figs. 2 and 3). In relative magnitude, the number and intensity of the seed release pulses was higher in the early part of the release interval, except in 2012, when the largest and longest release was in early August (Fig. 3). For duration, release events ranged from one to six days and most commonly extended over two days (Fig. 4). The minor release events tended to be short, but there was some variation (i.e. August 2010).

Over the four years, there were thus 18 seed release events and all followed rain events (Figs. 2 and 3). The rain events were generally substantial but this was not always the case (i.e. 2010 seed release 4, identified as '2010-4', and 2012-5). If a seed release commenced, it was apparently reduced with a rain event but some release persisted such as for events 2009-2 and 2013-5. The rain events may also confound the seed release observation since the overlook visibility would be obscured and the rain would wet the seed hairs, accelerating their settling.

As another possible hydrological cue, the possible coordination with changes in river discharge was investigated but there was little evidence for coordination in this river system (Figs. 2 and 3). With damming, the late spring peak along the lower Duncan River is substantially attenuated and there was only a single modest flow peak during the observed seed release intervals, with that

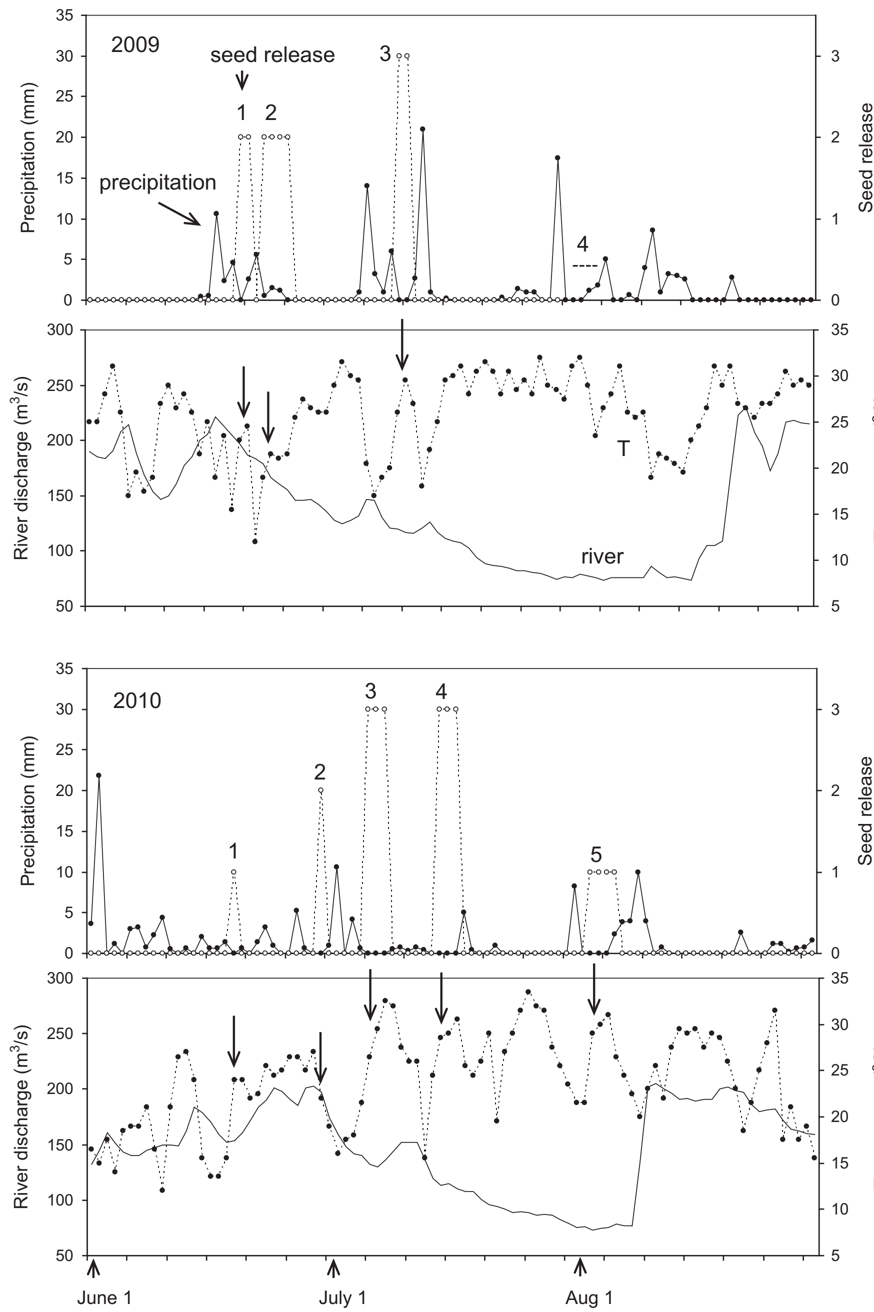

Fig. 2. Paired seasonal plots (June through August, *x*-axis ticks at 5 day intervals) of rain events and cottonwood seed release events (upper; 1–3 = slight to heavy) and Duncan River discharge and daily maximum temperature (lower) for four years (Fig. 2: 2009 and 2010; observations were not undertaken in 2011). The arrows in the lower plots extend down from the commencement of the numbered seed release events. In 2009, seed release monitoring was limited in August and thus the timing of '4' is uncertain.

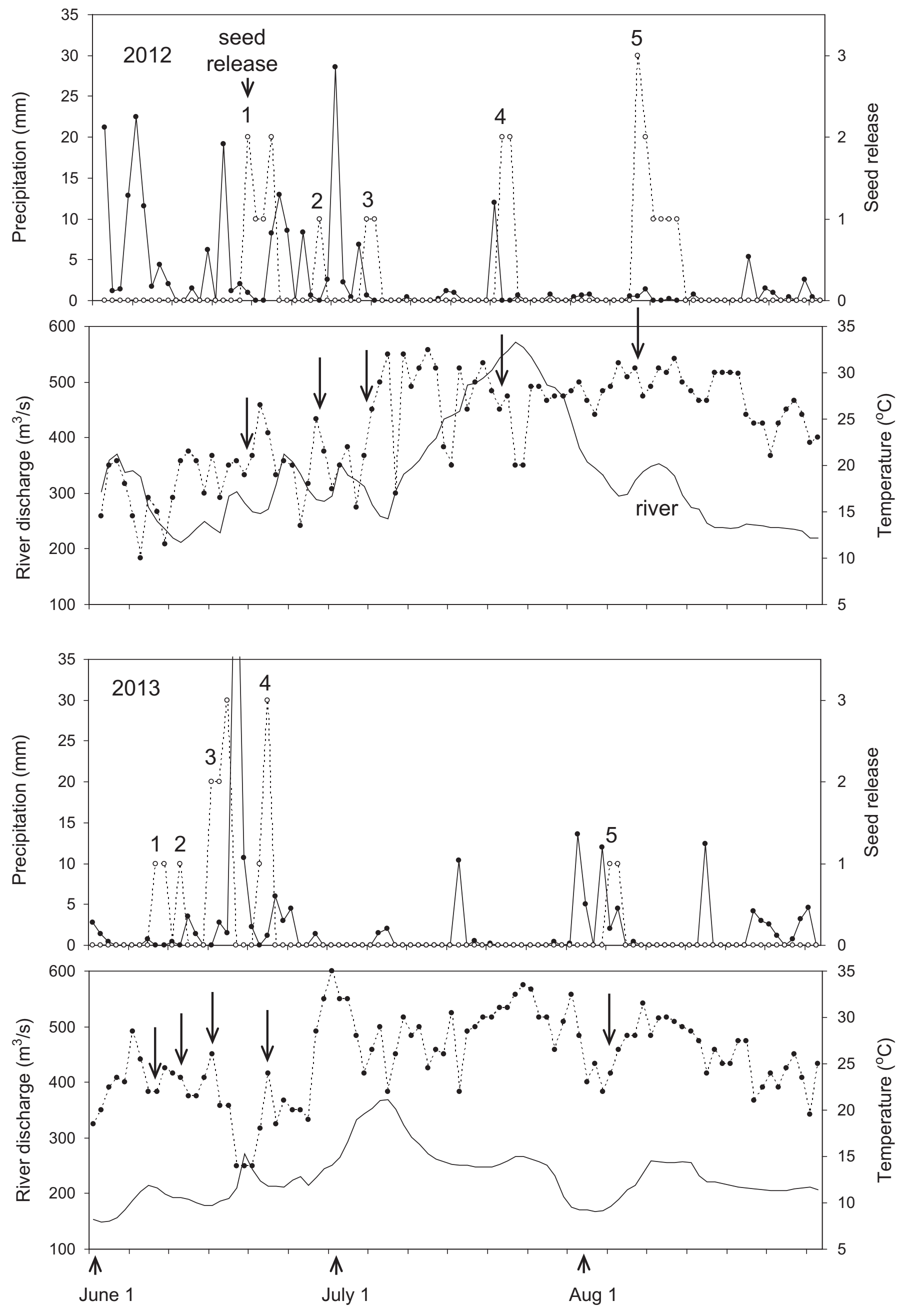

Fig. 3. Paired seasonal plots (June through August, *x*-axis ticks at 5 day intervals) of rain events and cottonwood seed release events (upper; 1–3 = slight to heavy) and Duncan River discharge and daily maximum temperature (lower) for four years (Fig. 3: 2012 and 2013; observations were not undertaken in 2011). The arrows in the lower plots extend down from the commencement of the numbered seed release events. In 2009, seed release monitoring was limited in August and thus the timing of '4' is uncertain.

being in July 2012 (2012-4). There was a seed release event associated with this river flow peak but there was also a rain event and the seed release followed both prospective cues.

With the subsequent contingency matrix, there were 61 time intervals over the four years and these were partitioned relative to rain and seed release. All 18 seed release events followed rain events but there were also 20 rain events that were not followed by seed release. There were 23 intervals without rain and there were no observed seed release events during these dry intervals. The subsequent Contingency Table χ^2 analysis provided a χ^2 value of 15.5, which is very highly significant ($p < 0.001$). Thus, the seed release events were not randomly timed over the prospective interval and instead, these consistently followed rain events. However, not all rain events triggered seed release and it appeared there were reduced seed releases after substantial seed releases. It also appeared that there was a final seed release in early August following considerable June or July release. In 2012 the August release differed in that it was heavy and not preceded by earlier releases.

Temperature was also considered as a third possible environment covariate or trigger. In this temperate climate region, rains generally occur during cooler weather and individual rain events are typically followed by warming, which is often substantial. This results in combinations of wet and cool, versus dry and warm conditions, somewhat confounding analyses of temperature and precipitation. There was a tendency for the seed release events to coincide with the post-rain warming and this occurred for 12 of

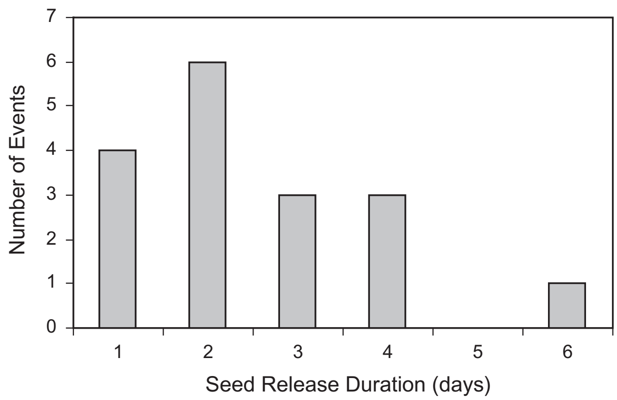

Fig. 4. The numbers of cottonwood seed release events of different durations over four study years along the lower Duncan River (excluding the indeterminate Aug 2009 event).

the 18 events (Figs. 2 and 3). However, there were also six seed release event that occurred without substantial warming and we tentatively conclude that rain was the primary cue that triggers seed release but it is also quite possible that temperature will influence the process, probably with post-rain warming further promoting seed release.

3.2. Observations of 'late seeders'

Along the Oldman, Elk, and Crowsnest rivers, we observed extensive seed release in June but minimal cottonwood seed release in July of 2014. The exceptions provided 'late seeders' that were rare in 2014, but occurred in two situations. In a coulee-draw extending down to the Oldman River in Lethbridge, two cottonwoods provided prolific and abrupt seed release in mid-July, about four weeks after the major seed release interval for that region. Based on leaf morphology, one tree was a balsam poplar (*Populus balsamifera*), which is very closely related to the black cottonwood, and the second was a natural hybrid *Populus x jackii* (*Populus balsamifera x Populus deltoides*). For both, there was fairly synchronous catkin maturation and seed release from the full canopy (Fig. 5), with no apparent differentiation of the crown versus lower limbs.

The second observation of late seeders included black cottonwoods along the shoreline of Island Lake, near the Crowsnest Pass along Highway 3 just east of the Continental Divide. Here, a cluster of trees were observed to be releasing seeds on July 14, 2014, well after the nearby trees away from the shoreline had already completed their seed release. The area was revisited July 21, 2014 to further explore the trees along the shoreline around the lake, and while no further seed release was observed, there were extensive deposits of fresh seeds indicating substantial release in the prior week. Island Lake is unusual in that is has limited surface outflow and instead there is gradual drainage through the fractured limestone bedrock around the lake. Consequently, this lake displays substantial change in the seasonal level, being high in the late-spring following the primary interval of snow-melt and rains, and it then recedes through the summer. The observed late season release in mid-July coincided with the lake level receding below the bases of the cottonwoods trunks, which would have also have inundated the root zones; this seed release was thus apparently associated with the removal of inundation stress.

4. Discussion

These results demonstrate that for black cottonwoods in a humid, temperate-climate mountain ecoregion, cottonwood seed

Fig. 5. Photographs showing a 'late seeder' *Populus balsamifera* tree, 15 July 2014, displaying complete seed release from the full canopy of this tree, about three weeks after the major seed release interval for most other trees at Lethbridge, AB.

release is a more dynamic process than had been expected based on the prior literature. Prior studies have often suggested a single dominant seed release peak. However, no prior study has included daily assessment, and with our increased temporal resolution, we observed four or five seed release events each year. If we had undertaken assessments such as with seed traps that were assessed weekly, or with weekly observations, we would have obtained outcomes similar to the prior studies. For 2009, there would have apparently been an initial larger release from the combination of events 1 and 2, followed by a second later peak from 3. For 2010, peaks 2, 3 and/or 4 might have been combined, dependent upon the sampling schedule. For 2012, peaks 1, 2 and 3 would have probably been combined, followed by later peaks 4 and then 5. And finally for 2013, peaks 1 through 4 would have probably been combined, and then the small 5 would follow later. The integration of seed release results over weekly time-steps thus misses the more complex temporal pattern, which revealed the apparent coordination with the hydration cue along this river system.

Even with a weekly time-step, some prior studies have determined that cottonwood seed release involves more than a single peak. With a similar climate and also with black cottonwoods, Meier (2008) observed a major peak with a minor secondary peak in northern Montana, USA. A similar pattern was observed by Gonzalez et al. (2010) for *Populus nigra* in Spain. Perhaps the most complete data set is provided by Stella et al. (2006) for *Populus fremontii* in California and that involved using binoculars for weekly viewing of catkins. With that weekly time-step there was a single major peak in 2003, but in 2004 the seed release was bimodal, and in 2002 the pattern was bimodal with the second peak in mid-July being larger than the first peak at the beginning of June. Precipitation patterns were not presented by Stella et al. (2006) and historic weather data accessed from the NOAA National

Climate Data Centre (http://cdo.ncdc.noaa.gov/ulcd/ULCD) indicated no precipitation for Modesto, CA in July 2002 or July 2004, as is typical for that region. This suggests that Fremont cottonwoods in the central valley of California have somewhat different environmental cues than the black cottonwoods along the Duncan River in British Columbia.

Since cottonwood seedling recruitment is typically limited by drought-induced seedling mortality (Cooper et al., 1999; Dixon, 2003; Polzin and Rood, 2006), it could be appropriate for hydration to provide an environmental cue for seed release. Thus, release after rain would allow the seeds to land on moist substrates, enabling water imbibition and subsequent germination. The coordination with rain might be especially suitable for a humid climate such as along the Duncan River, where cottonwoods are typically shallow-rooted and dependent upon rain, rather than being deeper-rooted phreatophytes that are reliant on the perennially-available alluvial groundwater (Rood et al., 2011). We might further anticipate that coordination with hydration might be broadly suitable for other riparian cottonwoods and for trees in semi-arid ecoregions such as the Fremont cottonwoods in California, river flow and stage might provide an alternative hydration cue. This view is consistent with the results of Stella et al. (2006) as increasing river flows were associated with the early seed release peaks in 2002 and 2004, and in the high-flow year of 2003 the seed release was more strongly coordinated with the peak, with the seed release peak occurring during the post-peak river flow recession.

Since water availability is a primary environmental factor that determines the distribution of trees and other plants, some coordination between seedling establishment and moisture would be expected. For many plants in drier ecoregions, mature seeds are released and there is subsequently a seed bank within the soil, and rain events enable imbibition and germination (Baskin and Baskin, 2001). This pattern is common in arid ecoregions such as deserts and semi-deserts, and there are subsequently pulses of germination, growth and reproduction following rain events (Baskin and Baskin, 2001).

The pattern that we propose for cottonwoods, and particularly for those adapted to humid ecoregions, is somewhat different. The cottonwoods seeds have very short intervals of viability after dispersal and there is thus no prospect of a perennial seed-bank. Instead, the near-mature seeds would be held by the maternal tree. With rain, on some trees or possibly some branches within trees, the catkins would complete ripening and release mature seeds, thus producing a seed release event.

This proposed pattern may be similar to some other serotinous plants, perennials and often woody shrubs and trees that retain mature seeds on the parent plant until some environmental trigger leads to their release (Baskin and Baskin, 2001). Hygriscence or hydriscence refers to serotiny that involves wetting as the environmental cue for seed release and this is not common, but displayed by some plants including some *Banksia* species and probably some cacti (Lamont et al., 1991; Rodriguez-Ortega et al., 2006). We might thus characterize black cottonwood as facultatively hygriscent as hydration, possibly in combination with warming, may trigger seed release. There may also be some release without this environmental cue, such as with the common release around the third week of June, which would generally occur after the natural timing of the peak flow and towards the end of the shoot growth season.

As we consider our results and those of prior studies we may develop an integrative model describing seed release in riparian cottonwoods. After flowering and pollination, seeds mature and subsequently in late spring near-mature seeds are produced by the female trees. However, rather than a single rapid and simultaneous seed release from the cottonwood groves, there are often two or more release events that may be influenced by environmental cues. For the black cottonwoods along the Duncan River, rain events and possibly post-rain warming might trigger the release of mature seeds, particularly from some trees. In some years such as for 2013 along the Duncan River and probably more commonly for some other cottonwood species and other rivers, the early pulse releases most of the seeds from that year (Table 1). For other years, the release could be more gradual or prolonged and could involve multiple release events of one to several days.

This maintenance of some of the seeds on the maternal tree could provide two advantages, with these overlapping with benefits with other serotiny strategies (Lamont et al., 1991). First, as already discussed, the staggered release would allow coordination with substrate moisture condition that is essential for seed germination and initial establishment. This would provide an opportunistic strategy for seed release. Second, the maintenance of near-mature seeds within the catkins could prolong seed vigor and viability, as occurs with some other serotinous plants (Lamont et al., 1991). Due to the small size and limited cotyledonary reserves the cottonwood seeds are short-lived after release and viability quickly declines (Karrenberg et al., 2002). The maintenance within the catkin could provide a favorable environment for the seeds and maternal support could continue. This would extend the interval of seed viability, consistent with the assessments by Guilloy-Froget et al. (2002). This strategy would thus provide vigorous seeds when the environmental conditions became favorably moist.

As a more speculative component, we further propose that in years in which there is not the sufficient sequence of environmental cueing for seed release, there may be a final purge of the remnant annual seed crop. Along the Duncan River this would occur in early August (Figs. 2 and 3) while along the Tuolumne River this may occur in mid-July (Stella et al., 2006; cf. Fig. 3). This might take place in association with the seasonal shoot growth cessation and terminal bud initiation, in advance of the late summer cold-hardening and associated leaf senescence and abscission of these deciduous trees. For this end-of-season purge we might further anticipate that declining photoperiod could provide an invariant seasonal cue, as it apparently does for the annual shoot growth cessation that is also on a determinate annual schedule (Böhlenius et al., 2006).

Our follow-up search for late-seeders in 2014, addressed the two subsequent questions. We did observe some late seeding trees elsewhere in 2014 but these were rare. Thus, late seeding occurs occasionally along multiple rivers but it is probably less extensive elsewhere than along the Duncan River. The late-seeding cottonwoods at Lethbridge also answered the second question, as there was extensive seed release from the full trees in July. Thus, late seeding involves particular individual trees, rather than being a later pulse from some branches or catkins within trees that would otherwise primarily release seeds earlier.

Following from these findings of the dynamic and environmentally-coordinated nature of seed release in cottonwoods, or at least in black cottonwoods, there may be considerations for cottonwood conservation and restoration. It is widely understood that floods promote cottonwood colonization and at least in dry regions it is likely that the floods are important for both fluvial geomorphic scour and deposition to create colonization sites, and also to provide a favorable moisture regime for seedling survival (Scott et al., 1996; Dixon, 2003; Rood et al., 2007). Consequently, in semi-arid ecoregions post-flood flow-ramping is important for seedling success (Rood et al., 2005).

Conversely, in a humid ecoregion the flood is still essential to generate barren seedling colonization sites but the flood recession and alluvial groundwater are probably less important for seedling establishment, since rain can provide the essential moisture for germination and seedling establishment and survival. This view is consistent with our prior conclusion for black cottonwoods along the free-flowing Elk River, also in southeastern British Columbia (Polzin and Rood, 2006). There, major floods are responsible for the development of colonization nursery sites but seedling recruitment was widespread on suitable barren substrates probably due to the moisture from local rains, rather than in association with the capillary fringe above the floodplain groundwater table (Polzin and Rood, 2006).

We thus propose that the environmental coordination of seed release is likely to be rather different in semi-arid regions, where summer rain is unreliable, versus humid regions, where sufficient rain supports cottonwoods not only in floodplain zones but also in upland areas following disturbance that creates barren colonization sites (Rood et al., 2007). And finally, relative to the current efforts to manage the Duncan Dam to provide environmental flows for black cottonwood recruitment, it is probably the geomorphic disturbance function from high flows that is essential to create colonization sites, while the summer flow patterns may be less important. In this humid ecoregions, rain, rather than alluvial groundwater, may provide a primary moisture source for riparian cottonwoods, including seedlings (this study) and the shallow-rooted mature trees (Rood et al., 2011).

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