Forest Ecology and Management 350 (2015) 22–29

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

Brenda Herbison [a,1], Mary Louise Polzin [b,1], Stewart B. Rood [c,*,1]

[a] North Kootenay Consulting, Argenta, BC, Canada
[b] Vast Resources, Cranbrook, BC, Canada
[c] University of Lethbridge, AB, Canada

ARTICLE INFO

Article history:
Received 16 January 2015
Received in revised form 1 April 2015
Accepted 22 April 2015
Available online 16 May 2015

Keywords:
Phenology
Populus
Riparian
River

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).

* Corresponding author. Tel.: +1 403 329 2327.
E-mail address: rood@uleth.ca (S.B. Rood).
[1] Three equal co-authors.

http://dx.doi.org/10.1016/j.foreco.2015.04.027

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'