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TECHNICAL NOTE

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Aspen recovery in northern Yellowstone: A comment on Brice et al. (2021)

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Abstract

Aspen sapling recruitment increased as browsing by elk decreased, following the 1995–96 reintroduction of wolves in Yellowstone National Park. We address claims by Brice et al. (2021) that previous studies exaggerated recent aspen recovery. We conclude that their results actually supported previous work showing a trophic cascade benefiting aspen.

KEYWORDS
aspen, elk, herbivory, recruitment, trophic cascade, wolves, Yellowstone

Brice et al. (2021), hereafter referred to as Brice et al., reviewed studies evaluating quaking aspen (*Populus tremuloides*) recruitment in northern Yellowstone National Park, following the 1995–96 reintroduction of grey wolves (*Canis lupus*) and subsequent reductions in browsing by Rocky Mountain elk (*Cervus canadensis*). They suggested these earlier studies "confounded understanding" of this textbook example of a trophic cascade, because researchers used heights of the five tallest (5T) young aspen in a stand (Figure 1) as an indicator of potential recruitment. We found that the results of Brice et al. actually supported the previous work they characterized as "biased" and "exaggerated," and their critique neglected relevant aspects of the ecological context (Beschta et al., 2023).

Considerable evidence of new aspen recruitment in northern Yellowstone has been based on 5T sampling (Beschta et al., 2018; Painter et al., 2014, 2015, 2018; Ripple & Beschta, 2007, 2012). The 5T method efficiently detected increases in heights of young aspen in stands that historically had been suppressed by elk browsing, thus allowing Ripple and Beschta (2007) to discern "the first significant growth of young aspen in over half a century." This result was ecologically important because overstory trees were dying without replacement (Ripple & Larsen, 2000), and studies in the 1990s had shown that young aspen were heavily browsed and rarely taller than 100 cm (Kay, 1990; Larsen & Ripple, 2005). In this context, the 5T method was useful for identifying stands where young aspen were growing taller and becoming saplings (>200 cm tall), thus more likely to become mature trees.

Stand regeneration depends on some young aspen growing tall, not the average height of all. The 5T method showed that saplings were present and growing taller in some stands but could not distinguish between stands with a small number of saplings versus stands with many (Figure 1). Random plots provided estimates of average height but could miss saplings in a portion of a stand (Figure 2). Painter et al. (2014)

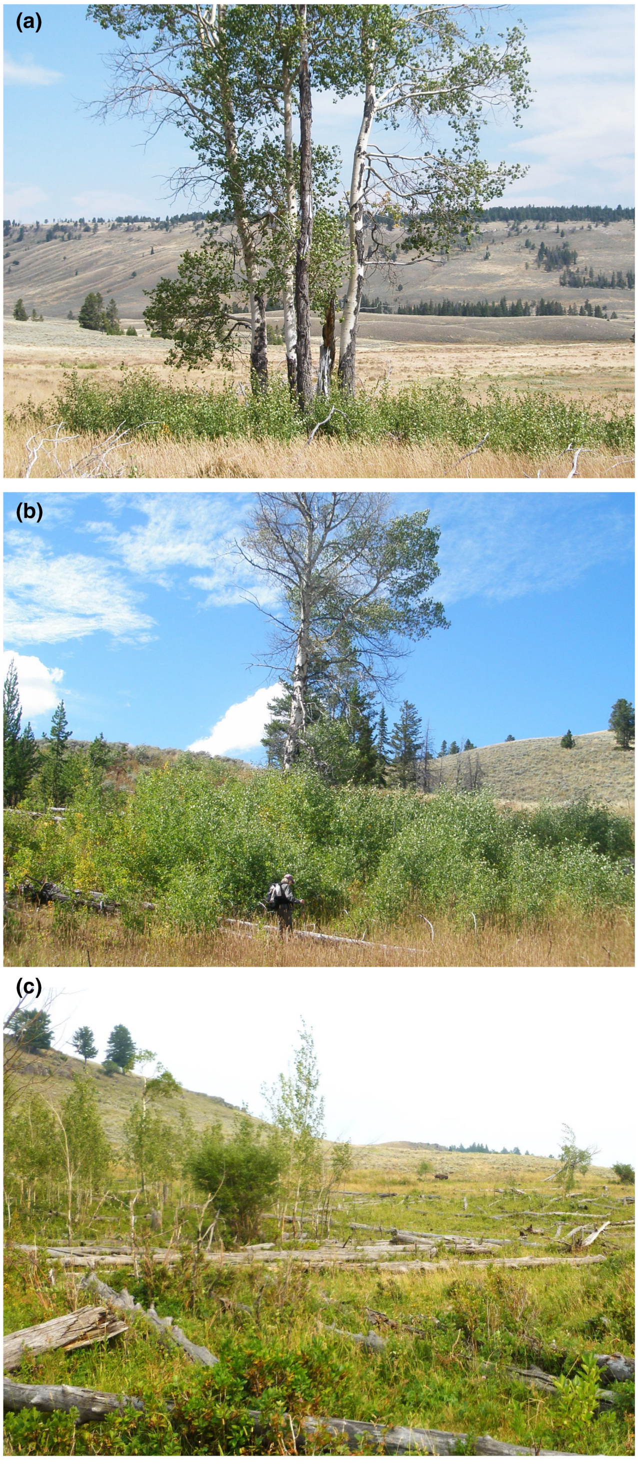

FIGURE 1 Aspen stands at various levels of recovery in Yellowstone National Park's northern elk winter range. Heights of the five tallest (5T) young aspen averaged 178 cm (a), 323 cm (b), and 680 cm (c) (R.L. Beschta and L.E. Painter, unpublished data). None of the young aspen in the stand in "a" exceeded 200 cm in height (an indicator of potential recruitment), whereas in "b" numerous young aspen had done so, and in "c" there was a patch of tall saplings but elsewhere most were <200 cm. In all three, the 5T approach efficiently identified the presence or absence of new saplings where, for decades, young aspen were suppressed by intensive browsing. In "a" and "b,", many plants were of similar height to the five tallest, while in stand "c" a group of young aspen were much taller than the rest in the stand, and these were missed by a random plot. Photos "a" and "b" are by R. L. Beschta, 2015; "c" is by L. E. Painter, 2020.

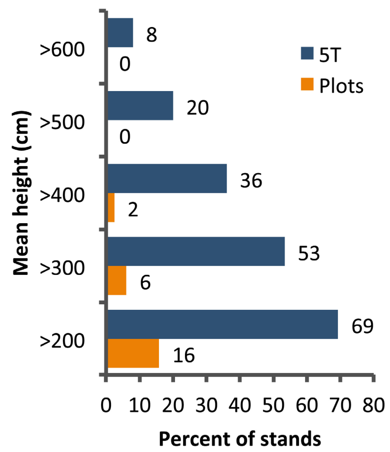

FIGURE 2 Percent of stands with young aspen exceeding the indicated mean height, in the year 2017, based on measurements of the five-tallest (5T) versus measurements from a single random plot (1 × 20 m), within each sampled stand. Clearly, the 5T approach provided a more sensitive indicator of new height growth and likely recruitment in the context of past recruitment failure, while random plots were a much more conservative indicator. For example, 69% of stands had an average 5T height >200 cm, whereas only 16% had an average young aspen height >200 cm in random plots. The 5T data also indicate that many stands had young aspen 300 cm or taller, and these heights are under-represented in small random plots. The much lower average height in random plots reflects the fact that stands with tall saplings may have many shorter plants, and the distribution of tall saplings may be patchy and missed by a small plot, as in Figure 1c (data source: Brice et al., 2021).

sampled random plots, similar to Brice et al., and found that 5% of young aspen were >200 cm in 2012, in 28% of stands, a small but significant increase from 0% in the same locations sampled in 1998. These results were reported as "widespread but patchy" sapling recruitment. Painter et al. and Brice et al. agreed about the mean or median height of young aspen in 2012 (about 90 cm), and both showed average height increasing over time but more slowly than the tallest (e.g., see Brice et al., figure 3).

Annual time series, based on growth and browsing scars of the 5T plants, further showed that young aspen heights increased as browsing decreased (Painter et al., 2014; Ripple & Beschta, 2007, 2012). Brice et al. objected that these trends may simply show that browsing decreased when these individual plants grew taller, perhaps because they had better growing conditions. However, their data collected over a series of years (figure 3 in Brice et al., 2021) confirmed previously published trends showing an increase in height over time. Similarly, Brice et al. supported the browsing estimates of Ripple and Beschta (2007) by showing there was little difference between random plots and 5T in 2007. Later work by Painter et al. (2014, 2015, 2018) did not include aspen taller than 200 cm in browsing estimates, thus avoiding this source of bias as more aspen grew above this typical elk browsing height.

The hypothesis that growth rates could account for differences in height, as suggested by Brice et al., was tested and rejected by previous studies (Painter et al., 2014, 2015; Ripple & Beschta, 2007). These tests found no relationship between leader length (an index of growth rate) and young aspen height. Instead, browsing differences remained the best explanation for height differences, consistent with other lines of evidence (Beschta et al., 2016; Painter et al., 2018).

Aspen researchers in northern Yellowstone sometimes asserted that 5T sampling provided a "leading edge" indicator of a broader aspen recovery. The central contention of Brice et al. was that this was false or exaggerated, yet they concluded that their own random sampling also "described a trophic cascade." Furthermore, no previous study claimed that a trophic cascade had "reverse[d] the deterioration of all aspen stands," only that many stands were again producing tall saplings, and that this was ecologically relevant. Given that the results of Brice et al. confirmed those of previous studies, their critique appears to be a, "glass half-empty," argument with no real difference, exaggerating claims of earlier work, and missing the importance of the ecological context. Whereas the 5T method was useful for detecting early changes in browsing and height of young aspen following wolf reintroduction, random sampling by Painter et al. (2014) and Brice et al. put these changes into a population context. Together, these methods produce a more complete description of the ongoing recovery of aspen in northern Yellowstone.

AUTHOR CONTRIBUTIONS

L.E.P., R.L.B. and W.J.R. wrote and edited the manuscript.

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DATA AVAILABILITY STATEMENT

No new data were used.

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