Short Communication: Aspen forest overstory relations to understory production

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LaRade, S. E. and Bork, E. W. 2011. **Short Communication: Aspen forest overstory relations to understory production**. Can. J. Plant Sci. **91**: 847–851. We examined the relationship between aspen cover and understory production across two topographic positions and two management systems within the Aspen Parkland of eastern Alberta. Understory biomass typically declined with increasing overstory, with greater yield losses on north-facing forests than bottomlands. Browse often compensated for herbage loss, and limited evidence of facilitative growth was observed.

Key words: Aspen removal, browse, competition, facilitation, herbage biomass, topographic position

LaRade, S. E. et Bork, E. W. 2011. **Brève Communication: Liens entre l'étage dominant de la forêt de trembles et la production du sous-étage**. Can. J. Plant Sci. **91**: 847–851. Les auteurs ont étudié les liens existant entre la forêt de trembles et la production du sous-étage à deux endroits et pour deux systèmes de gestion dans la tremblaie-parc de l'est de l'Alberta. La biomasse du sous-étage diminue habituellement à mesure qu'augmente celle de l'étage dominant, et les pertes de rendement sont plus élevées dans les forêts orientées au nord que dans les bas-fonds. Les espèces de broutage compensent souvent la disparition des herbages, et on observe des signes restreints d'une croissance plus facile.

Mots clés: Suppression des trembles, espèces de broutage, concurrence, facilitation, biomasse des herbages, emplacement topographique

Forage production in the Aspen Parkland natural subregion is variable due to plant community, soil and topographic characteristics (Wheeler 1976), and expansion of aspen (*Populus tremuloides* L.) into grasslands in this region has been widespread (Bailey and Wroe 1974). While the complexities of forest spread are not fully understood, changes in disturbance (Anderson and Bailey 1979), climate (Hogg et al. 2002) and resource availability (Powell and Bork 2007), either alone or in combination, may give aspen an advantage over other species.

Much attention has been given to understanding the effectiveness of aspen control, including herbicides (Hilton and Bailey 1974), fire (Anderson and Bailey 1979) and prescribed cattle grazing (Fitzgerald et al. 1986). Recent studies, however, have determined that aspen understories can provide considerable forage for livestock (Asamoah et al. 2004), with cattle even preferring these habitats (Asamoah et al. 2003).

Little is known about the specific role of aspen canopy closure on forage availability. Increased tree cover reduces light and water availability (Powell and Bork 2007), accounting for reduced forage growth (Bailey and Wroe 1974). However, moderate tree canopies may also enhance understory growth due to the moderation of climatic extremes and improved water use efficiency, the latter arising from reduced evaporation, greater relative humidity and lower associated vapor pressure deficits for the understory (Powell and Bork 2007). Consequently, the impacts of tree abundance on the understory are likely to vary depending on growing conditions. Favorable moisture within landscape depressions, for example, may reduce the competitive impact of trees during low rainfall.

Limited information also exists on the role of the intermediate shrub layer in altering forage productivity. While shrubs may directly benefit livestock by providing additional forage (Asamoah et al. 2004), they may also suppress underlying herbs that form the majority of conventional forage. As a result, clarification of the role of shrubs in contributing positively or negatively to cattle forage availability in Aspen Parkland landscapes is important to managing these forests.

Despite abundant information on aspen biology and ecology, no specific information exists on the relationship betweenaspen forest canopy closure and understory forage production, including the role of the shrub layer. We utilized an extensive network of sample plots to examine the empirical relationship between woody species abundance and forage production, including

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Abbreviations: **ANPP**, above-ground net primary production; **UC**, untreated check; **S&B**, spray and burn the role of shrubs in contributing to either herbage yield loss or total forage availability. Moreover, we assessed these relationships at each of two topographic positions within aspen stands managed with and without extensive forest control 25 yr prior.

Study Area

Sampling was done in east central Alberta at the 2700-ha University of Alberta Kinsella Research Station (lat. 53°0′N, long. 111°31.2′W). The station is located in the Aspen Parkland natural sub-region at 700 m elevation. The climate is cool continental, has average annual precipitation of 430 mm, with more than half from May to August, peaking in July (unpublished Environment Canada data, 1971–2000). The topography is undulating with numerous glacial moraine knolls and ridges intermingled with depressions. Area soils are Chernozems, Luvisols and Gleysols under grasslands, aspen forest and wet meadows, respectively (Wheeler 1976).

Dominant plant communities are representative of the Aspen Parkland and form a mosaic of habitats, including forest in depressions and north-facing positions, and open grasslands on south-facing uplands (Wheeler 1976). Forests include trembling aspen with limited balsam poplar (*Populus balsamifera* L.), an understory of shrubs such as western snowberry (*Symphoricarpos occidentalis* Hook.), wild rose (*Rosa* spp.), gooseberry (*Ribes* spp.) and Saskatoon (*Amelanchier alnifolia* Nutt.), and many herbs including smooth bromegrass (*Bromus inermis* Leyss.), Kentucky bluegrass (*Poa pratensis* L.), slender wheatgrass (*Agropyron trachycaulum* (Link) Malte), sedges (*Carex* spp.) and wild peavine (*Lathyrus* spp.).

Experimental Design

We utilized a network of 100 randomly located sample plots situated within forest distributed across five experimental pastures, each 16 ha in size. Pastures represented two contrasting management systems for aspen initiated in 1980, and included an extensive aspen control treatment in three pastures that involved aerial herbicide application (2,4-DB) followed by spring prescribed burning and broadcast seeding of tame forage (orchard grass, smooth brome, creeping red fescue and alfalfa) (Bailey and Irving 1984). Two other pastures were maintained as untreated checks. From 1980 to 2004, all pastures were managed as part of the station's rotational grazing system, with stocking rate at about 2 animal-unit-months ha^{-1}. Portions of the original check pastures were treated during the early 1990s with a low intensity prescribed burn. For consistency, we continue to refer to this treatment as the check.

Within each pasture, plots were further stratified by two topographic positions, including north-facing forests and bottom forests ($n = 10$ per position per pasture). While north-facing forests were on areas with a NE to NW aspect and slopes from 3 to 10%, bottom forests were generally level (<2% slopes) and adjacent to grasslands or wet meadows.

Field Sampling

During the summers of 2005 and 2006 (Jul. 10 to Aug. 02), each plot was sampled for total current above-ground net primary production (ANPP), including grasses, forbs and shrubs. Paddocks were ungrazed by livestock prior to sampling to ensure peak biomass was attained. Plots were widely distributed, providing a representative sample of aspen stands within which to quantify over-understory relationships. Plot locations from 2005 we repermanently marked and spatial coordinates recorded using a geographic positioning system to facilitate relocation in 2006.

During sampling, all plots were sampled for peak understory ANPP within a 0.25-m^2 (50 × 50 cm) sampling quadrat. Sampling was limited to a maximum height of 1.8 m to reflect accessibility for cattle. All ANPP of vegetation rooted within the plot was removed, sorted to grass, forb, and shrub components, dried at 50°C, weighed and converted to kilograms per hectare for analysis. Prior to harvest, total shrub cover (%) within each quadrat was quantified using an ocular estimate of crown closure. Additionally, cover of the tree overstory was assessed within a circular 2-m radius centered on the underlying plot: a larger sampling area was used for trees to account for patchiness in the overstory and the influence of any edge effects, for example through adjacent shading, on understory biomass. More specifically, aspen cover was obtained using four nested quadrats, each situated 1 m away from the central harvest quadrat in each cardinal direction, with their average used to provide a continuous tree cover per plot.

Statistical Analysis

All data were examined for homogeneity, with no transformations necessary. Linear least squares regression was used to assess the relationship between variation in understory ANPP and woody overstory cover within the untreated check (UC) and spray and burn (S&B) treatments. Three separate sets of regressions were performed, including the relationship between herb (i.e., grass + forb) biomass and both aspen cover alone and the cover of all woody species (i.e., trees and shrubs). Additionally, the comparative role of shrubs was assessed further by regressing total ANPP (i.e., herb + shrub current growth) against tree cover. Finally, separate regressions were done for each position and year to assess spatial and temporal variation in these relationships with changes in growing conditions.

Results

Among plots contained within the UC paddocks, relationships between understory biomass and the overstory were limited primarily to 2006, and were particularly strong within north-facing slopes (Table 1).

Table 1. Summary relationships between understory biomass (either herbage or total ANPP) and the percent cover of woody overstory (either aspen alone or aspen and shrub combined), within plots exposed to each of two management systems, at each of the north forest (NF) and bottom forest (BF) topographic positions, during each of two sampling years

Treatment	Position	Year	Overstory (X)	Response (Y)	R^2	*P* value	Relationship
Untreated check	NF	2005	Aspen	Herbage	0.18	***0.07***	**2449 − 66.6x**
		2005	Aspen	ANPP	0.07	0.28	3432 − 38.6x
		2005	Aspen + shrub	Herbage	0.02	0.55	2478 − 6.7x
	BF	2005	Aspen	Herbage	< 0.001	0.92	2609 − 5.6x
		2005	Aspen	ANPP	0.02	0.60	3081 + 26.4x
		2005	Aspen + shrub	Herbage	0.01	0.64	2829 − 9.0x
	NF	2006	Aspen	Herbage	0.36	***0.007***	**4841 − 98.0x**
		2006	Aspen	ANPP	0.21	***0.05***	**7775 − 115.4x**
		2006	Aspen + shrub	Herbage	0.53	***0.0004***	**7293 − 70.2x**
	BF	2006	Aspen	Herbage	0.01	0.66	5337 − 5.2x
		2006	Aspen	ANPP	0.0005	0.92	7066 + 9.2x
		2006	Aspen + shrub	Herbage	0.26	***0.02***	**8950 − 97.6x**
Spray & burn	NF	2005	Aspen	Herbage	0.07	0.19	1471 − 8.0x
		2005	Aspen	ANPP	0.03	0.36	2025 − 6.7x
		2005	Aspen + shrub	Herbage	0.18	***0.03***	**2003 − 9.6x**
	BF	2005	Aspen	Herbage	0.001	0.87	1849 − 2.3x
		2005	Aspen	ANPP	0.003	0.80	2362 + 3.5x
		2005	Aspen + shrub	Herbage	0.04	0.34	2152 − 7.3x
	NF	2006	Aspen	Herbage	0.02	0.53	2165 + 11.5x
		2006	Aspen	ANPP	0.14	***0.06***	**3473 + 71.3x**
		2006	Aspen + shrub	Herbage	0.0008	0.89	2251 + 1.5x
	BF	2006	Aspen	Herbage	0.1	0.11	2269 + 26.4x
		2006	Aspen	ANPP	0.15	***0.04***	**3922 + 58.3x**
		2006	Aspen + shrub	Herbage	0.004	0.75	2474 + 3.7x

At this location, herbage consistently demonstrated negative relationships with woody cover, with up to 53% variance in understory accounted for by the overstory. Moreover, these relationships were consistent regardless of whether they examined the tree component only, or included the intermediate shrub layer: reductions in herbage reached 70 kg ha^{-1} for each 1% increase in woody cover. Notably, the inclusion of shrub biomass in current annual growth was unable to compensate for herbage declines on north-facing slopes, as evidenced by the more pronounced negative relationship between total ANPP and aspen cover (ANPP declined by 115 kg ha^{-1} for each 1% increase in aspen) (Table 1).

Similar results were evident in bottom forests of the UC treatment, with marked decreases in herb biomass under increasing woody cover (Table 1). Unlike north-facing slopes, however, the inclusion of shrub biomass within estimates of ANPP compensated for herbage decreases under increasing aspen cover of bottom forests, leading to no association between total ANPP and tree cover (Table 1).

Few relationships existed between the understory and overstory during 2005 in the S&B treatment, particularly bottom forests (Table 1). Within north-facing slopes of this treatment, total herbage had a modest decline of 9. 6 kg ha^{-1} for each 1% increase in combined cover of shrubs and aspen. Despite this, total woody cover accounted for only 18% of variance in herbage biomass, suggesting other factors were responsible for the variation in herbage at this location. Also notable within north-facing slopes of the S&B, was that inclusion of shrub biomass in ANPP appeared to offset losses associated with herbage decline, as this relationship was no longer significant (Table 1).

Finally, similar results appeared 1 yr later during 2006 within both north-facing slopes and bottomlands of the S&B. At both positions, no relationship was evident between herb biomass and total woody cover. However, when shrub contributions were included, total ANPP increased with forest cover by 72 and 58 kg ha^{-1} for each 1% increase in aspen at the north-facing and bottomland locations, respectively (Table 1).

Discussion

Previous studies have found reduced productivity under high tree densities (Burrows et al. 1990; Powell and Bork 2007), largely due to competition between trees and herbs for moisture and light. Reduced herbage found here under aspen highlights the competitive nature of this tree species and its ability to decrease grazing opportunities, with greater reductions within the UC treatment where aspen remained at or near its maximum canopy closure under limited disturbance.

Despite the negative influence of aspen, inclusion of shrub production in estimates of forage availability altered many overstory–understory relationships, even to the point of producing similar or compensatory total ANPP responses across forests of varying closure. Contribution of shrubs to production appeared to offset the suppressive influence of trees on understory herbage, provided those shrubs increasing produced biomass that remained suitable for livestock consumption.

Differences in overstory–understory relationships were also evident between years, with more marked suppression of the understory in 2006. Weaker relationships during 2005 may reflect growing conditions. Although total annual precipitation was similar between years, spring rains in 2006 were more timely and associated with warmer temperatures, and may have accelerated tree leaf-out and the loss of light, thereby leading to more negative relationships between the tree overstory and understory. Conversely, poorly timed moisture and cool weather appeared to reduce herbage in 2005, and may have limited competition from the overstory, as both the frequency and intensity of precipitation influence plant growth (Robertson et al. 2009).

Marked differences were expressed between the impact of aspen on north-facing slopes and bottomlands in altering understory production, including herbaceous and shrub components. Understory suppression was greater on north-facing slopes, particularly in the UC treatment under dense aspen. The extensive overstory at this location, particularly during the growing conditions of 2006, may have reduced light and water simultaneously, thereby leading to the more negative impact on the understory. Moreover, the inability of shrubs to compensate for herbage declines within north-facing slopes of the UC suggests that tree cover reduced production at this location by impacting herb and shrub components. Thus, reduction of aspen to increase forage appears more important on north-facing slopes, where competition may be expressed more strongly.

Similar to north-facing forests, bottom forests of the UC also exhibited negative relations between herbage and woody cover, with one difference: inclusion of shrubs into estimates of ANPP compensated for herbage loss, suggesting competition from the overstory may be lower in bottom forests. There are several explanations for this observation. Bottom forests were situated where the understory could access near-surface soil moisture (Wheeler 1976), reducing competition for water. Similarly, bottom forests were on landscape positions with little to no slope, and can, therefore, be expected to have more favorable light, which may have made this resource less limiting for understory growth than in north-facing forests. Although herbs and shrubs may compete with one another, changes in herb abundance within the bottom position appeared offset by improved shrub production, thereby stabilizing ANPP. This same pattern of shrub compensation was evident on north-facing slopes of the S&B, and could have been facilitated by the previous reduction in forest cover arising from historical aspen control treatments.

Differences in the type and intensity of competition between overstory and understory within bottomlands may also explain the divergent responses at this location between landscape treatments (i.e., herbage was negatively associated with woody species in the UC, and positively in the S&B). Within UC plots, total herbage was elevated under low woody cover (8950 kg ha^{-1}), only to decline sharply under an increasing woody canopy. Furthermore, the strongest negative relationship was observed when both shrubs and trees were included suggesting both detrimentally impacted total herb biomass. Given the abundant moisture in 2006 and the lack of significant relationships the year prior, we hypothesize that the competition apparent during 2006 may have been related not to moisture, but instead to limitations in light within the understory of these heavily forested plots created by the absence of previous disturbance. This is further supported by the notion that bottomlands should have had ample moisture in both years due to runoff and an elevated water table (Wheeler 1976).

Herbage within bottomlands of the S&B treatment exhibited a markedly different relationship to the overstory. Total ANPP in these plots was low, and subsequently increased in relation to increasing aspen cover. There are several explanations for this observation, including that understory and overstory growth were correlated, but dependent on another, as of yet unaccounted for, environmental factor not measured in the current investigation. However, another explanation is that ANPP may have been improved under trees (Frost and McDougald 1989). A partial aspen canopy can favor the understory by reducing frost (i.e., lengthening the growing season), conserving water (by lowering temperatures and associated evaporation), and promoting water use efficiency (by lowering water vapor differentials) (Powell and Bork 2007).

Overall, our results suggest that the degree of tree canopy closure coupled with growing conditions, specifically landscape position and yearly rainfall, may influence the nature of the relationships between understory production and the tree overstory within the Aspen Parkland. Moreover, these relations were variable with mostly negative but occasionally positive impacts on the understory, with contributions from shrubs potentially offsetting herbage declines under an increasing aspen canopy. Further research is warranted to more fully understand the impacts of aspen on understory forage availability.

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