

Utah State University

DigitalCommons@USU

Aspen Bibliography

Aspen Research

1958

Production of herbaceous vegetation in openings and under canopies of western Aspen

L. Ellison

W.R. Houston

Follow this and additional works at: https://digitalcommons.usu.edu/aspen_bib



Part of the [Forest Sciences Commons](#)

Recommended Citation

Ellison, L., Houston, W.R. 1958. Production of herbaceous vegetation in openings and under canopies of western Aspen. *Ecology* 39(2):337-345.

This Article is brought to you for free and open access by the Aspen Research at DigitalCommons@USU. It has been accepted for inclusion in Aspen Bibliography by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.



PRODUCTION OF HERBACEOUS VEGETATION IN
OPENINGS AND UNDER CANOPIES OF WESTERN
ASPEN

By

LINCOLN ELLISON AND WALTER R. HOUSTON

Reprinted from *Ecology*, Vol. 39, No. 2, April, 1958

PRODUCTION OF HERBACEOUS VEGETATION IN OPENINGS AND UNDER CANOPIES OF WESTERN ASPEN

LINCOLN ELLISON¹ AND WALTER R. HOUSTON²

Intermountain Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Ogden, Utah

Extensive forests of quaking aspen (*Populus tremuloides* Michx.), which occur widely at intermediate elevations in the Intermountain and Rocky Mountain West, constitute an important resource, both esthetically and economically. The aspen type is esteemed among sightseers, picnickers, and campers because of its beauty. Aspen forests protect the soil of an important snow-collecting belt on western mountain watersheds. Although aspen is not one of the important timber species, aspen wood products are in considerable and increasing demand. Finally, the type supports undergrowth capable of furnishing a great amount of cover and forage for wildlife and livestock. On aspen range in good condition one may wade waist deep through a rich mixture of many plants, including species of *Heracleum*, *Mertensia*, *Delphinium*, *Osmorhiza*, *Agastache*, *Erigeron*, *Rudbeckia*, *Senecio*, *Thalictrum*, *Agropyron*, *Bromus*, *Elymus*, and *Carex*. Most aspen range in the Intermountain region is depleted from prolonged overgrazing, however, and palatable species that were formerly abundant are likely to be scarce or absent.

Curiously, much less vegetation is produced in openings, as a rule, than beneath the aspen canopy.³ Usually the vegetation of openings is the sparser and shorter, and it tends to include a smaller proportion of desirable forage species (Houston 1954). It may, indeed, include undesirable species such as the annual *Madia glomerata* Hook., that are absent under the aspens. We have personally observed such differences in production and species composition on aspen ranges in Utah, Nevada, southern Idaho, western Wyoming, and western Colorado. These observations have included a great variety of sites with respect to soil and exposure, and many variations in character of vegetation.

Why should such a difference in ground-cover

¹ Deceased (March 9, 1958).

² Field Crops Research Branch, Agricultural Research Service, U. S. Department of Agriculture, Miles City, Montana.

³ The herbaceous vegetation in a narrow zone within the edges of some aspen stands, where livestock "shade up," may be more severely depleted than vegetation in the open, but this is not true under aspen canopy generally.

production exist? Is it a product of those factors responsible initially for the existence of openings in an aspen forest? Is it caused by differences in microclimate under and away from the aspen canopy? Is it a result of heavier grazing in openings than under the aspen? Or is it the result of interactions between some or all of these factors?

Whatever the cause, this widely observed difference seems anomalous, because it would appear that demands upon the environment by the aspen trees themselves might be expected to infringe on the needs of plants of the shrub and herb layers. Logically, therefore, being free of such competition, the openings should produce more vegetation, not less, than equal areas under aspens. Such a relation has been described by Moinat (1956) in the *Quercus gambelii* type in southwestern Colorado, a zone somewhat warmer and drier than the aspen-fir zone. Moinat shows that production of the field layer in grassy parks is markedly higher than in scrub-oak thickets.

Many trenching experiments (reviewed by Korstian and Coile 1938) have demonstrated the adverse effects of root competition by forest overstory on growth of native ground vegetation or artificially planted trees. Shirley (1945), in a study carefully designed to test the relative effects of shade and root competition of aspen and jack pine on tree seedlings and planting stock in Minnesota, demonstrated a root-competitive depression of conifer growth, although not of survival. Shirley's comment is that, "In these studies, however intense the root competition of the overwood, its effect on survival was more than offset by the benefits of the shade, provided this did not reduce the light intensity below 20 percent." We know of no experiments of this kind involving western aspen except for Pearson's (1914) comparisons of survival of planted Douglas-fir under aspen and in openings. These showed better survival under aspen.

METHODS

The present study was designed to measure the productivity of herbaceous vegetation beneath aspen canopies and in adjacent openings where basic site factors appeared to be the same. Grazing by livestock was excluded, but deer had access to

three of the four study sites, and rodents and rabbits to all four. The study areas were spaded up and seeded artificially so that the same species could be compared. In order to evaluate the competitive effects of aspen roots, additional plots under the aspen trees were trenched.

The study was begun in the fall of 1950 at four sites ranging in elevation from 8,050 to 9,000 feet in Ephraim Canyon in central Utah. These four sites pretty well bracket the continuous aspen type in Ephraim Canyon, although isolated patches of aspen occur both at lower and higher elevations. Nine plots, each 10 feet square, were laid out at each site. Six plots were placed under the aspen canopy in pairs, and three were placed in opening 25 to 75 feet away from the aspen edge. The plots under aspens were so placed as to avoid unnecessary removal of trees.

One member of each pair of plots under aspens was trenched in the fall of 1950 to a depth of about 18 inches to cut the aspen roots. This treatment also cut any roots of the shrubby and herbaceous undergrowth that might have extended into the trenched plots. The trenches were then refilled with soil. Trenching, followed by refilling, was done each year during the course of the study.

Each plot was divided into four subplots 5 feet square, and each subplot was seeded to a different species, using seed collected in Ephraim Canyon. Four native species were used: *Bromus carinatus* Hook. & Arn., *Elymus glaucus* Buckl., *Rudbeckia occidentalis* Nutt., and *Heraclium lanatum* Michx.

Each subplot was planted with five rows 5 feet long and 1 foot apart. All data were taken from the inner three rows, ignoring 0.9 foot at each end and the outer two rows to avoid border effect. This left 9.6 square feet as the area of each subplot.

Seeding was done in the fall of 1950 at a rate of about two seeds per inch of row. In the spring of 1951, all stands were thinned to one plant per 2 inches of row, and that fall bare spots were reseeded. The plantings were weeded periodically.

Considerable difficulty was experienced in getting stands on all plots, particularly the open plots. Full stands were important to success of the comparison, since we were concerned with measurement of differences in productivity rather than differences in success of germination or of seedling establishment. Because full stands were not achieved uniformly, the plantings were rated in 1952 and 1953 on a scale from 0 to 5 as to abundance and distribution of plants. In the comparisons that will be made, only the better stands, classes 3, 4, and 5, will be used—except in those

instances where a poor stand outproduced a stand having a higher rating.

In the fall of 1951, the grasses *Bromus* and *Elymus* were harvested at a height of 1 inch, and their weights were used as part of the data for a preliminary report (Houston 1952). The clipping treatment did not appear to hurt *Bromus*, but it seems likely that some plants of *Elymus* were killed and the stands thereby reduced. In the fall of 1952 the weight of all species was estimated (Pechanec and Pickford 1937). In September 1953 all plants were harvested to ground level. The herbage was taken into the laboratory in paper sacks and brought to air-dry weight. These weights, expressed in grams per 9.6 sq. ft. (or, multiplied by 10, in pounds per acre), form the basic data used in this report. They consist of three components: (a) the species planted, (b) weeds persisting in spite of cultivation, and (c) estimates for losses from current utilization by deer and rabbits. For most harvests, components (b) and (c) were not large, but including them gives a closer approximation to true production than would be possible if they had been omitted.

Total precipitation during the growing seasons of 1951 and 1952 was slightly above average, and in 1953 it was materially greater than average (Table I). September precipitation was below

TABLE I. Monthly precipitation in inches at Headquarters during the three growing seasons of this study, 1951 to 1953, in comparison with the average

| | Average 1934-48 incl. | 1951 | 1952 | 1953 |
|----------------|-----------------------------|------|------|-------|
| May..... | 2.02 | 2.85 | 3.00 | 4.27 |
| June..... | 1.82 | 1.27 | 2.69 | 0.34 |
| July..... | 1.57 | 1.41 | 1.14 | 4.83 |
| August..... | 1.50 | 2.81 | 1.08 | 1.12 |
| September..... | 1.24 | 0.21 | 0.48 | 0.13 |
| Seasonal..... | 8.15 | 8.55 | 8.39 | 10.69 |

average in all 3 years, but precipitation so late in summer, when most herbage has dried adds little to plant growth. The spring of 1953 was very late. Because of a late storm, snow did not leave the open plots at the lowest area until May 14 and at the highest area until June 6. Scantiness of precipitation during June was therefore not so harmful to plant growth as it might be in some years. Precipitation was well distributed during July and August. It seems probable, therefore, that the 1953 season, the year of harvest, was an especially good one for plant growth.

Temperature records show nothing distinctive about the three growing seasons except that min-

ima tended to be lower than average in both 1951 and 1953.

Climatic observations were not made at the individual study areas. From long-time records in Ephraim Canyon it may be estimated that average daily temperatures are about 3.5° F. lower at the highest station than at the lowest (Price and Evans 1937). Average annual precipitation may be estimated to vary from about 23 inches at the lowest station to 27½ inches at the highest, and growing-season precipitation, May through September, from about 7 to 8 inches (Lull and Ellison 1950). These values have been computed from relations determined over a much greater elevational range; between our four sites they may be modified materially by local topographic factors. For example, the highest site with a westerly exposure and the next highest with a southerly exposure may well be warmer than the two lower sites with near-level northerly exposures.

RESULTS

Table II shows that production of *Bromus carinatus* on the untrenched plots under aspen was materially less than on either the trenched plots under aspen or on the open plots. Both differences, which are statistically significant ($P < .01$), are illustrated in Figures 1 and 2. From these differences it would appear that the natural potential for production of *Bromus* in aspen openings is greater than under an aspen canopy, and that aspen root competition—together with root competition of surrounding shrubs and herbs—is important in depressing yields of undergrowth.

TABLE II. Air-dry production of *Bromus carinatus*, in grams per 9.6 square feet, at four sites in Ephraim Canyon, 1953

| Site and elevation | UNDER ASPEN | | Open |
|--------------------------|-------------|------------|------|
| | Trenched | Untrenched | |
| Bluebell (9,000 ft.) | 171 | 30* | 128 |
| Headquarters (8,800 ft.) | 133 | 58 | 116 |
| Snowberry (8,450 ft.) | 97 | 17 | 47 |
| Aspen (8,050 ft.) | 89 | 36 | 51 |
| Weighted average | 122.5 | 35.9 | 85.5 |

*Average from 2 subplots only. See Table III and text.

In 1951 yields were about one-fifth of those in 1953, averaging 22.9, 5.3, and 21.7 grams for the trenched, untrenched, and open treatments respectively. Estimated yields in 1952 tended to be intermediate between yields of 1951 and 1953. The question may well be asked, therefore, whether maximum production had been achieved in the third year. Possibly it had not; but it is also unlikely that production would have increased

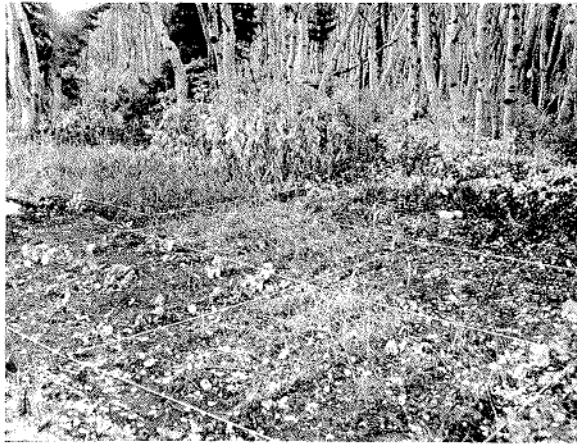


FIG. 1. Untrenched (foreground) and trenched plots at Snowberry Sept. 26, 1953, just before harvest. The trenched plantings show marked release from overstory root competition. Nearest untrenched subplot was planted to *Bromus*, subplot to left of it to *Rudbeckia*, to right of it to *Heracleum*, and directly behind it to *Elymus*. Adjacent trenched subplot was also planted at *Elymus*, to left of it to *Bromus*, to right of it to *Rudbeckia*, and directly behind it, with some of the large leaves barely visible through the grass, to *Heracleum*. Upright frame is 1 meter square.



FIG. 2. An open (untrenched) plot at Snowberry, Sept. 26, 1953, just before harvest. *Bromus* is in left foreground, *Rudbeckia* in right background. On this plot the stand *Elymus* (left background) is very poor, and no stand of *Heracleum* (right foreground) has been obtained, despite use of a straw mulch upon a repeat seeding. Upright frame is 1 meter square.

greatly in subsequent years because much of the rise in production the third year can be attributed to an unusually favorable growing season.

In 1953 plants on the trenched plots were markedly taller (88 cm) than plants on the untrenched plots (68 cm); and the latter were about the same height as the much heavier plants on the open plots (67 cm).

There is also a suggestion in Table II of increasing production with increasing altitude.

Open yields ($r = .82, P < .01$) and trenched yields ($r = .62, .05 > P > .01$) are significantly correlated with altitude, but untrenched yields are not. Thus, whatever the favorable factors that increase with altitude in this study (probably precipitation and insolation), it appears that aspen root competition masks their influence on the ground cover. Perhaps this means that the aspen is dominant over other vegetation in a physiological as well as a physiognomic sense.

One of the untrenched plots at Bluebell gave materially higher yields than the others (Table III). This yield of 189 grams is more than twice as great as that on any of the other 11 untrenched plots of *Bromus* in this study, and is of the order of the yields from the trenched plots. Yields of other species on this plot were also exceptionally high in 1953; estimated yields of all species were markedly higher on this plot than on the others in 1952; and the clipped yields of *Bromus* and *Elymus* in the seedling year 1951 were also higher on this plot than on the others. Although this aberration was puzzling at first, an examination of the overstory aspen in 1953 provided the explanation: most of the trees surrounding this particular plot had died! In 1955 only 6 living trees 1 inch DBH and over were within 10 feet of the edges of this plot, whereas there were 17 trees within the same distance from each of the other two untrenched Bluebell plots. Essentially, then, the plot may be considered to have been freed from aspen competition about as effectively as if it had been trenched. For this reason, the data from this plot are excluded from Table II and from corresponding tables for the other three species. The plot does have value, however, if the foregoing explanation is valid, in corroborating the effects of trenching.

TABLE III. Air-dry production of *Bromus carinatus* at Bluebell, in grams per 9.6 square feet, 1953

| | UNDER ASPEN | | Open |
|--------------|-------------|------------|-------|
| | Trenched | Untrenched | |
| | 117 | 26 | 157 |
| | 230 | 34 | 124 |
| | 167 | 189 | 104 |
| Average..... | 171.3 | 83.0 | 128.3 |

Yields of *Elymus glaucus* (Table IV) show the same essential relations as those of *Bromus*. Production on the trenched plots greatly exceeds production on the untrenched plots under aspen ($P < .01$). Average production in the open is greater than on the untrenched plots under aspen at the two upper sites, but the difference is not

statistically significant. Nevertheless, taking into account the fact that all the open plots are not fully stocked, it seems probable that the potential for production of *Elymus* is greater in the open than under aspen. Open stands that had been rated fair to good at Snowberry in 1952, and that had been rated poor to fair at Aspen, had too few plants left by the fall of 1953 to warrant harvesting.

TABLE IV. Air-dry production of *Elymus glaucus*, in grams per 9.6 square feet, at four sites in Ephraim Canyon, 1953

| Site and elevation | UNDER ASPEN | | Open |
|-------------------------------|-------------|------------|-------|
| | Trenched | Untrenched | |
| Bluebell (9,000 ft.)..... | 264 | 75* | 124† |
| Headquarters (8,800 ft.)..... | 110 | 34 | 57† |
| Snowberry (8,450 ft.)..... | 84 | 14 | |
| Aspen (8,050 ft.)..... | 109 | 50 | |
| Weighted average..... | 141.7 | 40.1 | 90.5 |

*Average from two subplots only. †Some subplots not fully stocked.

In 1951 yields of *Elymus* on the trenched aspen and open plots were the same, 27.8 grams; on the untrenched plots under the aspen they were only 5.7 grams. Estimated yields in 1952, as with *Bromus*, were intermediate between yields of 1951 and 1953.

In 1953 at Bluebell and Headquarters, *Elymus* plants on the trenched plots were tallest (102 cm) and on the open plots shortest (81 cm). Plants on the untrenched plots were intermediate in height (87 cm). This, taken together with their light weight, reflects the characteristic spindliness of untrenched plants.

A suggestion of increasing *Elymus* production with increasing altitude exists in Table IV. Trenched yields are correlated significantly with altitude ($r = .59, .05 > P > .01$). Too few outside yields are available, with the variation that exists, to give a significant correlation. Untrenched yields, as with *Bromus*, show no correlation with altitude, suggesting again that aspen root competition obscures the relation.

Yields of *Rudbeckia occidentalis* in the open average a little higher than those on the trenched plots under aspen (Table V); both are significantly greater ($P < .01$) than yields on the untrenched aspen plots. If the open plots had been fully stocked, it seems probable that they would have materially outproduced the trenched plots under aspen. Estimated yields in 1952, which were somewhat lower, tended to show the same relations.

Production on the trenched and open plots in

TABLE V. Air-dry production of *Rudbeckia occidentalis*, in grams per 9.6 square feet, at four sites in Ephraim Canyon, 1953

| Site and elevation | UNDER ASPEN | | Open |
|-------------------------------|-------------|------------|-------|
| | Trenched | Untrenched | |
| Bluebell (9,000 ft.)..... | 288* | 42* | |
| Headquarters (8,800 ft.)..... | 130 | 44 | 236 |
| Snowberry (8,450 ft.)..... | 186 | 8 | 186† |
| Aspen (8,050 ft.)..... | 156 | 86* | 214*† |
| Weighted average..... | 180.8 | 41.3 | 211.4 |

*Average from 2 subplots only. †Some subplots not fully stocked.

1953 shows a slight positive correlation with altitude, but neither is statistically significant.

The average of 86 grams for two untrenched subplots at Aspen is probably unduly high. One of the subplots was flooded by runoff from a road and produced 145 grams, more than five times as much as the other.

Two bits of evidence indicate that the blank in Table V, and probably the poor stocking of the open plots at the two lower stations, were due to difficulty in initial establishment, rather than to unfavorable growing conditions for established plants. First, the three *Rudbeckia* plants growing on the three open plots at Bluebell in the fall of 1953 were very robust. The same can be said for plants on the understocked plots at Snowberry and Aspen. Second, *Rudbeckia* grows naturally and abundantly in openings throughout the aspen zone, and particularly at Bluebell.

Much of the differences in weight between treatments in 1953 is created by differences in numbers of *Rudbeckia* flower stems. Plants on the untrenched aspen plots produced few stems, and a high proportion of these produced no flower heads. These plants averaged only 55 cm in height. The taller, more robust plants on the trenched aspen plots (82 cm) and on the open plots (81 cm) produced abundant, heavy stalks bearing a high proportion of heads.

Yields of *Heracleum lanatum* are 10 times as high on the trenched plots under the aspen as on the untrenched plots (Table VI). The difference is significant statistically ($P < .01$), and is compounded of two factors, a difference in size of plants, and a difference in stocking. *Heracleum* plants were over twice as tall on the trenched plots (13 cm) as on the untrenched plots (6 cm), and they were almost twice as numerous—59 per plot as compared with 33.

None of the untrenched plots had fully stocked stands, and it therefore appears that the competitive effect of aspen was marked not only in terms of plant size, but in a material difference

TABLE VI. Air-dry production of *Heracleum lanatum*, in grams per 9.6 square feet, at four sites in Ephraim Canyon, 1953

| Site and elevation | UNDER ASPEN | | Open |
|-------------------------------|-------------|------------|-------|
| | Trenched | Untrenched | |
| Bluebell (9,000 ft.)..... | 60 | 4*† | |
| Headquarters (8,800 ft.)..... | 23* | 5*† | |
| Snowberry (8,450 ft.)..... | 42 | 3† | |
| Aspen (8,050 ft.)..... | 20*† | 4*† | |
| Weighted average..... | 39.2 | 3.7 | |

*Average from 2 subplots only. †Subplots not fully stocked.

in successful seedling establishment. This effect of aspen on stand establishment is also reflected by the other species, but by none so sensitively as by *Heracleum*.

In 1952 estimated yields, although lower than 1953 yields, showed the same essential difference between treatments as in 1953.

The trenched plots show a positive correlation between altitude and production, but this is not significant statistically. A positive correlation between altitude and abundance of plants per plot is significant, however ($r = .81$, $P < .01$). The corresponding correlations for the untrenched plots are much weaker, as has been noted with production of other species.

No full stands of *Heracleum* were produced on the open plots, and most open plots had no plants of *Heracleum* at all in the fall of 1953. The plants that were present in 1953, however (on two plots at Bluebell and two plots at Headquarters), were thriving and large. Their robust growth was doubtless partly a result of reduced competition, for these few plants had the cultivated area of their subplots to themselves; but it also indicated that the limiting factor in these plantings of *Heracleum*—at the two uppermost sites, at least—was connected more with difficulty in seedling establishment than with the species' inability to grow in the open.

Observations Since 1953

The plots have been observed during the 3 years since 1953, although trenching and weeding have been discontinued. The differences noted from 1951 to 1953 have persisted through 1956. On the open plots in 1956 *Bromus* and *Rudbeckia* were vigorous, but most of the *Elymus* had disappeared. The differences in vigor of plants on the trenched and untrenched plots under the aspen were still visible (Fig. 3). A rough attempt was made in July 1956 to compare the volume of herbage produced on the trenched and untrenched plots with that produced by the undisturbed un-



FIG. 3. The same two plots as in Fig. 1, on Aug. 26, 1956. Even 3 years after trenching there is markedly greater growth on the trenched than on the untrenched plot. *Rudbeckia* and *Heracleum* (left and right foreground, respectively) have increased in size since 1953. Upright square-meter frame is between untrenched *Elymus* to this side and trenched *Elymus* behind.

dergrowth. The comparison was highly subjective because different species were involved. The open plots did not appear to be producing so great a volume of herbage as the adjacent mixed native vegetation. In general it seemed as if the trenched plots were still producing somewhat more, and the untrenched plots somewhat less, than the undisturbed undergrowth. It seems evident, therefore, that by 1956 the roots of aspen and its undergrowth had not reasserted themselves in the trenched plots, and that the seeded herbaceous vegetation in the untrenched plots, both in the open and under aspen, had not yet built up the vigor possessed by the native vegetation.

The lesson to be learned from these observations is one of caution in applying the results of a short-term study. The seeded vegetation on the untrenched plots is evidently not in equilibrium with the aspen, even 6 years after planting, in the way that the mixed, undisturbed native vegetation is. If the study were to continue for several decades, in other words, presumably the plants on the untrenched plots would be able to secure a greater share of their needs from the soil at the expense of aspen (as undisturbed herbaceous plants presumably do now), and the difference between their production and production of plants in the open would be lessened somewhat. We do not think this difference would cease to exist, however.

DISCUSSION

Insofar as a short-term study can reveal the facts, it seems clear that the potential for production of herbaceous vegetation in aspen openings is greater than that beneath the aspen canopy. It is

also clear that a factor limiting production under the aspen is root competition from the aspen trees themselves, or from its undergrowth—or at any rate some factor associated with these roots—since production on the trenched plots was consistently greater than production on the untrenched plots. Except where full stands were not achieved, these patterns were essentially the same for all four species and for all 3 years in which observations were made.

What would competition under aspen be for? The most obvious answer is the soil moisture that trenching releases to the undergrowth. Our only soil-moisture measurements were made at a depth of 3 to 6 inches September 10, 1951, the seedling year. They showed that soil moisture was somewhat higher on the trenched than on the untrenched and open plots (Houston 1952), but it seems unlikely that any such difference would be great with full stands of ground vegetation to utilize the soil moisture. Other studies have also shown soil moisture to be greater on trenched than on untrenched plots (e.g., Fricke 1904, Craib 1929, Korstian and Coile 1938, Shirley 1945).

It is doubtful whether competition for nutrients would be material under the conditions of this study because the fall of aspen leaves, twigs, and gum should return to the soil annually a large part of the nutrients currently being taken up by the trees. It is noteworthy, however, that other trenching experiments (Korstian and Coile 1938, Wallihan 1940) have indicated that soil nitrogen may be slightly greater on trenched than on untrenched plots. This may be a consequence of slightly greater soil moisture.

Shirley's (1945) experiments suggested to him "that factors other than light and soil moisture may be involved in the competition of the under-vegetation" with coniferous transplants, and he suggests exudation of toxic substances. Possibly aspen roots inhibit the growth of herbaceous plants by exuding harmful substances or by harboring harmful organisms, but this experiment can throw no light on the question. Some living aspen roots persisted on the trenched plots, as evidenced by sprouts that had to be cut out periodically, but they were probably not numerous enough to balance this influence, if it was an influence, of aspen roots on the untrenched plots.

Unfortunately no trenching was done to evaluate the effects of root competition from woody and herbaceous vegetation surrounding the open plots. These effects may have been material on the open plots since there were shrubs, mainly *Symphoricarpos oreophilus*, in the vicinity of most of them.

The poor showing made by *Elymus* and *Heracleum* in the open plots may indicate that these species require shade and are unsuited to openings. We think this is unlikely: both species are known to grow well in openings in association with other herbaceous species, although their establishment may be slow. Certainly the failure of *Rudbeckia* in the open plots at Bluebell cannot be explained in these terms, because it has invaded much comparable overgrazed range. Deficiencies in experimental technique—difficulties in getting seedlings established on the bare, unshaded soil of the open plots—are believed chiefly responsible for the poor stands of these three species.

In light of the fact, established by trenching, that severe competition under aspen reduces herbage production below that of the open, let us return now to the original question: why is the reverse commonly observed, that production under aspen is greater than production in openings?

The most obvious way to explain the differences in production would be to relate them to causes—whatever they may be—of so sharp a contrast in type as that between aspen stands and openings. Unfortunately we do not know why aspen stands and openings exist as they do, so the patterns cannot help in explaining the observed differences in productivity. In many areas it is obvious that aspen is spreading vegetatively into openings, although often the invasion is held in check by browsing of the new shoots by grazing animals. This tendency suggests that the causes of the type boundaries are historical rather than environmental, and that differences in site are not such as to prevent occupancy of the openings by aspen. In some areas, however, the aspen edge appears to be static or nearly so, and the hypothesis of a site difference is more tenable. The tendency for invasion is marked at the Bluebell, Headquarters, and Aspen sites of this study, but not at the Snowberry site.

Differences in topography can be ruled out, for commonly there is no change in exposure or degree of slope between an aspen stand and an adjacent opening. Openings seem to occur under all the variations in slope and exposure where aspen forests are found.

No comprehensive comparison of soils under aspens and in adjacent openings has been made, so far as we are aware, and therefore, although the soils in a particular situation appear to be essentially the same, it cannot be stated categorically that this is so. We have observed in central Utah that aspen may be growing on shallow, rocky limestone soils, while deeper soils nearby are

dominated by herbaceous vegetation; but this difference is not invariable. There is no clear indication that inherent soil differences are great enough or consistent enough to account for the marked differences that generally exist in the ground vegetation.

The aspen stand itself produces differences in the soil as compared with herbaceous openings. The ground surface under aspen receives a layer of litter from the annual fall of leaves and twigs, as well as litter from the undergrowth, and during the summer there is a constant dripping of aspen gum which eventually finds its way to the soil surface. This litter, together with the canopy itself, protects the soil within aspen stands from erosion. The soil surface of openings, in contrast, receives relatively little aspen litter, and, in consequence of denudation by overgrazing during the past century, many openings have lost considerable topsoil. Thus the obvious differences in soil appear to be more an effect than a cause of the two types of cover.

It is also obvious that microclimate is different in the two habitats. The openings are relatively sunny, warm, and windy; atmospheric humidity is lower, and evaporation near the soil surface is much greater than under the trees (Pearson 1914, Marston 1956). While the soil surface of openings receives more precipitation than the soil surface beneath the tree canopy, because of less interception loss, this difference is probably offset by greater loss of moisture through evaporation. On the other hand, aspens themselves use soil water, and presumably quite a lot, since they are characteristic of fairly moist sites. This use has been measured in northern Utah near the upper limits of the aspen type. The combined water consumption of aspen and its undergrowth there, together with evaporation loss, was estimated to be about 4 inches more per year than evapo-transpiration in nearby herbaceous, perennial vegetation (Croft and Monninger 1953). In that study much of the aspen drain was below the root level of the herbaceous undergrowth, but some of it was no doubt from the upper 4 feet of soil occupied by roots of forbs and grasses.

In short, although herbaceous vegetation may find some advantages in the environment under aspen (greater atmospheric humidity, more fertile topsoil), the advantages of more light and especially more soil moisture in the open appear to outweigh them. But if this be so, should not production under aspen be less, rather than more, than in openings? The experimental results reported here indicate that it should. Except when there was stand failure in the open, and in spite

of possible root competition from vegetation surrounding the open plots, production was always higher in the open than on untrenched plots under the aspen.

The differences in production commonly observed are probably a result of differences in grazing pressure. It may be generally observed that livestock, particularly cattle and to some extent sheep, graze in openings more heavily than they graze under aspen. This impression was checked in 1955 by utilization studies on eight sites in and near Ephraim Canyon (Bailey 1956, pp. 75-78). At each site utilization was found to be greater in openings than under the trees, both early and late in the season. While degree of use varied with time of year, plant species, range condition, and class of grazing animal, by fall the utilization was usually two to four times as heavy in the openings as under the aspens. The reason for this difference is probably that the unshaded forage plants in the open manufacture more sugars than plants in the shade of trees, and are therefore relished more by the animals (Welton and Morris 1928, Plice 1951, 1952).

That grazing may be the decisive factor is also suggested by other evidence. First, in stands that have escaped heavy grazing for many years, and that are therefore presumed to be near pristine condition, production in the openings appears to be greater than under the aspen (Houston 1954, Table 2, Area X). Unfortunately such ungrazed areas are few and small, and are mostly in rough, rocky terrain that is not typical of the broad aspen type. Second, the differences in ground vegetation, both in amount and kind, between openings and aspen stands, tend to be greatest where grazing has been heaviest and range condition is poorest. Finally, it may be observed generally that when grazing is reduced on depleted aspen range, desirable plants increase first under the aspens and then spread out into the openings. This has been observed with such grasses as *Bromus carinatus* and *Agropyron trachycaulum* which work out of the aspens to invade openings dominated by *Madia glomerata*, and with such highly palatable forbs as *Osmorhiza occidentalis*, *Mertensia leonardi*, *Valeriana occidentalis*, and *Heracleum lanatum*.

It is probable that microclimatic effects associated with severe grazing make difficult the regeneration of moisture-loving species in openings. These effects include the loss of foliage shade from tall herbs (among which are the more moisture-loving, succulent, and palatable species); loss of litter and baring of the soil surface to the full heating and drying effects of sun and wind:

loss of soil structure and damage to seedlings because of excessive trampling; and in many places accelerated erosion of the topsoil itself. Because of these effects, shorter, more xeric, less palatable species come to dominate heavily grazed openings. Thus, both directly and indirectly, a difference in severity of grazing appears to be the mechanism by which the contrast in herbage production between openings and under aspen is produced.

That the potential for herbaceous production in openings is greater than under the aspen canopy has at least two important applications in range management:

(a) If the range manager finds production in openings to be as great as or greater than production under the aspens, and particularly if the preferred forage species are about equally abundant, he has reason to believe that the range is producing near its maximum and that it is in good or excellent condition. If production is materially poorer in openings than under the aspen, he has reason to believe that the range is not producing as much as it should, and that it is in fair, poor, or very poor condition, depending primarily upon species composition. In any event, if soil in the openings is bared excessively or shows evidence of accelerated erosion, the range is in unsatisfactory condition (Ellison, Croft, and Bailey 1950). Thus the range manager may use the production of aspen undergrowth as a first approximation to the potential productivity of nearby openings. His estimate may be far from the true productivity if the range has been heavily overgrazed for many years, but he can assume that the openings should be *at least* as productive of herbaceous and shrubby vegetation as the aspen stand.

(b) Because they are the more heavily grazed, the more easily depleted, and the more difficult to restore, openings are the key areas for management of aspen range for livestock. If their productivity and soil stability can be improved or maintained, it is almost certain that the condition of the adjacent range under the aspen canopy will be satisfactory.

SUMMARY

In order to evaluate the potential productivity of aspen openings and the ground vegetation under aspen, plots established in openings and under aspen canopy at four sites were seeded with *Bromus carinatus*, *Elymus glaucus*, *Rudbeckia occidentalis*, and *Heracleum lanatum*. Yields at the end of the third season furnish the basis for this report. In order to evaluate the effect of root

competition from aspen, paired sets of plots were trenched to cut the aspen roots.

Plots in the open were much more productive than untrenched plots under aspen, indicating that the potentiality for production in openings is greater than under aspen. (A complication was introduced by the fact that full stands were less consistently attained on the open plots than in aspen shade. This is believed to be a reflection of faulty technique rather than of inherently lower productivity in the open.) The most consistently successful species was Bromus; the least, Heracleum. The results of this study are confirmed by natural areas in which production of herbaceous vegetation in aspen openings appears to be greater than within the aspen stand.

Trenched plots were much more productive than untrenched plots under aspen, which suggests that the principal factor in depressing yields under the aspen is root competition. These effects were still visible 3 years after trenching was discontinued.

A tendency was noted for increased production with increasing altitude. This trend may be related to an estimated increase of 1 inch in summer (May through September) precipitation between the lowest and highest sites, and to warmer exposures at the upper two than at the lower two sites. The trend was noted on the trenched, and to a lesser extent on the open plots, but in no case on the untrenched plots. This suggests that the environmental benefits associated with altitude (e.g., increased precipitation) are more readily taken advantage of by the trees than by their undergrowth.

Utilization of forage by livestock is heavier in openings than under an aspen canopy. Throughout the aspen type this difference in use intensity, together with the more adverse microclimatic effects associated with heavy grazing in openings, is believed to be responsible for the poorer production and species composition commonly noted in openings than under the aspen canopy.

Relative production under aspen canopy and in adjacent openings can be used as an aid in judging range condition. The openings are "key" areas for management.

REFERENCES

- Bailey, Reed W. 1956. Annual report of the Intermountain Forest and Range Experiment Station, Forest Service, U. S. Dept. of Agriculture, 110 pp., processed.
- Craib, Ian J. 1929. Some aspects of soil moisture in the forest. Yale Univ. School Forestry Bul. 25, 62 pp.
- Croft, A. R., and L. V. Monninger. 1953. Evapotranspiration and other water losses on some aspen forest types in relation to water available for stream flow. Trans. Amer. Geophys. Union 34: 563-574.
- Ellison, Lincoln, A. R. Croft, and Reed W. Bailey. 1951. Indicators of condition and trend on high-range-watersheds of the Intermountain Region. U. S. Dept. Agr. Agricultural Hdbk. No. 19, 66 pp.
- Fricke, K. 1904. "Licht und Schattenholzarten," ein wissenschaftlich nicht begründetes Dogma. Centbl. f. das Gesam. Forstw. 30: 315-325. U. S. Forest Service translation, 1934, 30 pp., typewritten.
- Houston, Walter R. 1952. A preliminary study of some factors affecting herbage production in the aspen type of central Utah. M.S. Thesis, Univ. of Utah, 27 pp., typewritten.
- . 1954. A condition guide for aspen ranges of Utah, Nevada, southern Idaho, and western Wyoming. Intermoun. Forest and Range Expt. Sta. Research Paper 32, 25 pp., processed.
- Korstian, Clarence F., and Theodore S. Coile. 1938. Plant competition in forest stands. Duke Univ. Forestry Bul. 3, 139 pp.
- Lull, Howard W., and Lincoln Ellison. 1950. Precipitation in relation to altitude in central Utah. Ecology 31: 479-484.
- Mar ton, Richard B. 1956. Air movement under an aspen forest and on an adjacent opening. Jour. Forestry 54: 468-469.
- Moinat, A. D. 1956. Comparative yields of herbage from oak scrub and interspersed grassland in Colorado. Ecology 37: 852-854.
- Pearson, G. A. 1914. The role of aspen in the reforestation of mountain burns in Arizona and New Mexico. Plant World 17: 249-260.
- Pechanec, Joseph F., and G. D. Pickford. 1937. A weight estimate method for the determination of range or pasture production. Amer. Soc. Agron. Jour. 29: 894-904.
- Plice, M. J. 1951. Sugar versus the intuitive choice of foods by livestock. Agron. Jour. 43: 341-342.
- . 1952. Sugar versus the intuitive choice of foods by livestock. Jour. Range Mangt. 5: 69-75.
- Price, Raymond, and Robert B. Evans. 1937. Climate of the west front of the Wasatch Plateau in central Utah. Monthly Weather Rev. 65: 291-301.
- Shirley, Hardy L. 1945. Reproduction of upland conifers in the Lake States as affected by root competition and light. Amer. Midl. Nat. 33: 537-612.
- Wallihan, F. 1940. Factors affecting the response of forest vegetation trenching (abstract). Jour. Forestry 38: 223-224.
- Welton, F. A., and V. H. Morris. 1928. Woodland pasture. Jour. Forestry 26: 794-796.