

Carbohydrate Concentrations in Honey Mesquite Roots in Relation to Phenological Development and Reproductive Condition

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Highlight: Lower concentrations of total available carbohydrates were found throughout the growing season in roots of honey mesquite trees with many flowers and pods than in trees with a low reproductive potential. Following bud burst, during the period of pod elongation, mesquite trees with few reproductive organs replenished the root tissue with carbohydrates faster than did trees bearing many reproductive organs. During the seed development phase of growth, a second decline in root carbohydrate concentrations occurred. This decline began approximately 1 week later in the heavily fruited trees compared to the trees with few pods. Variation in carbohydrate storage among trees differing in reproductive potential largely explains why it is difficult to consistently kill mesquite roots with growth regulating herbicides. When carbohydrates are no longer accumulating in the roots of trees with few flowers or seed pods, those trees with many reproductive organs may be accumulating carbohydrates. Since herbicides such as 2,4,5-T move to the roots when carbohydrates are accumulating, little herbicide would get to the roots in the one case. Optimum herbicide application dates for West Texas would generally occur from May 15 to June 15 and from July 1 to July 15.

Since the introduction of phenoxy herbicides in the 1940's, much attention has been given to chemical control of honey mesquite (*Prosopis glandulosa* var. *glandulosa*). The susceptibility of woody plants to systemic herbicides, such as the phenoxy, appears to depend on the season of the year or the stage of growth (Fisher et al., 1956; Leonard and Crafts, 1956; Tschirley and Hull, 1959). In order to kill some brush species and deep-rooted perennial weeds, foliar-applied herbicides must be translocated to the root system (Mitchell and Brown, 1946; Basler, 1962), which has been correlated with carbohydrate movement from the foliage to the roots (Beatty, 1953; Carter and Chappell, 1957; Dalrymple and Basler, 1963; and Badiei et al., 1966). Herbicide accumulation in honey mesquite roots is essential to obtain complete destruction of plants of this species since it commonly resprouts from dormant basal buds after injury to the top growth. Since phenoxy herbicides move in association with carbohydrates in the phloem (Crafts, 1956; Yamaguchi and Crafts, 1959), a correlation of the phenology of the tree and root carbohydrate concentrations as an indication of carbohydrate movement would be a helpful indication of the

proper time to spray herbicides for maximum kill. Previous work by Fisher et al. (1959) described average carbohydrate concentrations in the root tissue as influenced by season of the year, but variations in carbohydrate accumulation patterns as influenced by differences in phenological development which commonly occur among trees were not separated.

The basic objective of this study was to correlate reserve carbohydrate concentrations of the roots to phenological stage of development and to compare reserve carbohydrate concentrations of plants of the same phenological stage but differing in reproductive loads.

Study Area and Methods

The study area was located 4 miles south of Grassland, Tex., on the Post-Montgomery Ranch. Level topography characterized the site, and the soil was an Amarillo fine sandy loam.

Soil moisture is the critical environmental factor limiting plant growth in the area. Mean annual precipitation is less than 50 cm, with 70 to 80% falling between May and October.

Data used in this study was obtained monthly from November, 1970, through March, 1971, weekly from April 2, 1971, through July 26, 1971, biweekly during August, 1971, and monthly in September and October, 1971. On each sampling date, soil samples were taken in 15-cm increments to a depth of 60 cm at three random locations within the study area. Soil moisture content of these samples was determined by gravimetric analysis. Using mercury-filled glass laboratory thermometers, soil temperatures were obtained at 15-cm increments to 60 cm. Ten to twelve honey mesquite trees ranging in height from 1.3 to 2.1 m were randomly selected at each sampling time. The phenological development of each tree was recorded and later related to the reserve carbohydrate concentration of the root tissue. Some trees had as many flowering spikes as they had leaves, while other trees had few, if any, flower spikes. Trees with as many or more flower spikes as leaves were assumed to have maximum reproductive potential; thus, they were assigned a reproductive potential value of 100. Trees with fewer than the maximum reproductive organs were rated with lesser values according to the proportion of flowers possessed. If a tree had no flowers, its reproductive potential was rated zero. Values above 50 were referred to as plants with high reproductive potential; those below 35, as plants with low reproductive potential (Fig. 1). Trees with values between 35 and 50 were not sampled. A summary of the phenological stages recorded during the 1971 growing season is given in Table 1.

For this study, only root carbohydrates were determined. Trees store carbohydrates also in the root crown and the stems. However, the major objective of this study was to find out when carbohydrates were withdrawn and restored to root tissue as a guide to when foliar applied herbicides could translocate to the roots. Time did not permit analyses from all storage organs, hence only the roots were included.

To collect root tissue for carbohydrate analysis, soil was

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The report is College of Agricultural Sciences Publication Number T-9-140. Texas Tech University.

Manuscript received August 7, 1974.



Fig. 1. Variations in reproduction common between honey mesquite trees. (left) Few reproductive organs; (middle) Many reproductive organs (flowers); (right) Many reproductive organs (beans).

excavated from around each tree's root crown to an approximate depth of 0.7 m. The basal crown was removed at the point where it became relatively narrow and perpendicular to the earth's surface, usually at a depth of 30 cm. Root tissue measuring approximately 11.5 by 4.0 cm was then obtained using a power saw or wood chisel. Bark was removed from the sample so only xylem tissue was actually collected. Tissue samples were immediately placed upon dry ice to minimize enzyme activity during transport to the laboratory. Soil was removed from the tissue samples before placing them in a forced-air oven for 1 hour at 90°C for enzyme inactivation. Drying was continued for 48 hours at 65°C. After drying, the heartwood of the root tissue was separated from the sapwood and discarded. The samples were ground in a Wiley Mill to pass through a 40-mesh screen and then analyzed for total available carbohydrates (TAC). Smith et al. (1964) defined TAC as those carbohydrates that are readily available as a source of energy to the plant. Included are the sugars, dextrans, fructosans, and starch but not structural carbohydrates such as cellulose and hemicellulose. The TAC were extracted from the plant material as described by Smith et al. (1964) except that 0.2 N HCl was used instead of 0.2 N H₂SO₄. The carbohydrates were determined using the anthrone reagent and spectrophotometry (Murphy, 1958) with glucose as the

standard.

Results

Analyses of all trees sampled between November 14, 1970, and October 22, 1971, showed a maximum root carbohydrate concentration of 20.6% (dry weight basis) on December 15, 1970, the first sampling date, by which time all leaves had abscised. The TAC gradually declined during winter dormancy to 15.9% on April 9, 1971, due to respiration and possibly root growth. The minimum carbohydrate concentration of 9.7% occurred on May 24, 1971 (Fig. 2). Variability among samples was relatively low as the standard error was less than 10% for all of the 25 means except five which were between 10 and 15% of the mean.

Honey mesquite trees initiated visible new growth during the third week of April despite relatively dry soil conditions (Fig. 2). Immature flower spikes were produced concurrently with new leaves. Trees with small, furled leaves (0.6 to 1.9 cm) and trees without new leaves were sampled on April 16. The TAC root concentration of trees exhibiting leaves averaged 12.3% while the TAC concentration of trees which had not yet produced leaves averaged 19.8%. This latter TAC concentration is considerably higher than that shown for April 9 because on that date it was impossible to tell visibly which trees would leaf out early and which would develop later. Thus, the April 9 values represent no stratification according to phenological development such as was done on April 16. This lower TAC concentration in the roots of trees leafing out early indicates that expanding leaves and rapid twig elongation depend, at least in part, on reserve carbohydrates stored in the root tissue of honey mesquite trees. However, if the beginning of rapid root growth coincides with bud break in April, part of the reserve carbohydrates undoubtedly move to the growing root tip, and this would also result in a decrease in the root's carbohydrate content.

By April 30, bud burst was rapidly occurring and the root carbohydrate concentration declined to 13.4% (Fig. 2). The mesquite leaves were light green and three-fourths unfurled (7.6 to 9.0 cm). Fisher et al. (1959) also reported a similar decline in mesquite root carbohydrates immediately following bud burst. On May 10, mesquite trees possessed fully extended leaves, spikes with white flowers, and immature flower spikes;

Table 1. Honey mesquite's phenological development during the 1971 growing season.

November, 1970- March, 1971	Trees dormant.
April 16, 1971	Most mesquite trees had begun to leaf out. Leaves were furled and immature flower spikes were less than 2.5 cm in length.
May 10, 1971	Trees possessed fully extended leaves, white flowers, and immature flower spikes.
May 24, 1971	Aging yellow flowers predominated with relatively few white flowers remaining. Immature (green) flower spikes were still present on many trees. Green pods less than 2.5 cm long were first noted.
June 7, 1971	Pods varying in length from 2.5 to 15.2 cm were present along with yellow flowers.
July 5, 1971	Maturing pods (seeds one-half developed) were the only reproductive organs left on the trees.
August 26, 1971	Pods had fallen from trees.
September- October, 1971	Trees with leaves but physiologically inactive.

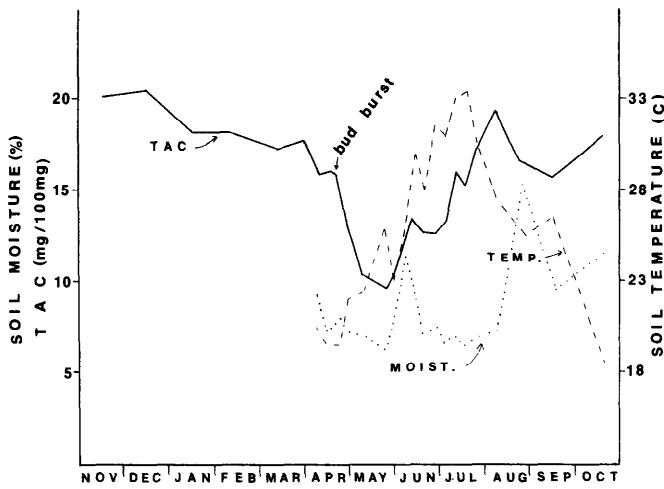


Fig. 2. Total concentration of available carbohydrates (TAC) in honey mesquite roots for a calendar year (1970-71); also, soil moisture and soil temperatures for the 30-45 cm depth is shown for the growing season 1971.

the carbohydrate concentration of root tissue sampled this date had declined to 10.4%. The minimum carbohydrate content in root tissue occurred May 24, when flower spikes with aging yellow flowers predominated, but many immature flower spikes also remained on most trees. Pods less than 2.5 cm long were recorded on May 24, and in 2 weeks the small pods elongated to approximately 15 cm. From May 24 to June 14, a replenishment of root carbohydrates occurred to a peak of 13.6%. During this period, mesquite trees possessed immature flower spikes, yellow flowers, and elongating pods varying in length from 2.5 to 15.2 cm. Seed formation within pods was not obvious until the last week of June, and this phenological stage corresponded to a second drop in reserve carbohydrates similar to that characteristic of honey mesquite plants at time of bud burst (Fig. 3). Relatively few flowers remained on the trees at this date and pods were the dominant reproductive organs present. The mesquite pods matured during July, and most pods had fallen from the trees by August 9.

Influence of Fruiting Load

All trees sampled from May 10, 1971, to July 26, 1971, were separated into two groups: (1) trees with a relatively large potential for reproduction (>50), and (2) trees which failed to produce any or relatively few flowers and pods (<35) for this particular growing season. Sampling variation during this period was relatively small as the standard error values mostly ranged from 1 to 12% of the means. Only four samples out of 22 had standard errors in excess of 14% of the mean. Carbohydrate analyses indicated that honey mesquite trees with a high percentage of flowers and pods had a lower reserve carbohydrate concentration in the roots than did trees with few or no reproductive organs throughout the growing season (Fig. 3). From May 10, 1971, through July 26, 1971, trees with many flowers or pods averaged 10.9% in TAC concentration, while trees which largely failed to produce reproductive organs averaged 15.8% TAC.

Honey mesquite trees with a high reproductive potential exhibited a minimum root carbohydrate concentration of 9.2% on May 24. These trees possessed mature yellow flowers, green flower spikes, and immature pods approximately 2.5 cm long. A build-up of carbohydrates in the root tissue peaked at

13.1% on June 22. A second decline in reserve carbohydrates resulted in a minimum of 9.3% on July 5 (Fig. 3). Although no data are available from this study, we feel that this decline was caused by a stimulation of growth, especially root growth. Shoot and root growth are known to alternate in some tree species (Reed and MacDougall, 1937; Rogers and Head, 1968). *Robinia pseudoacacia* and *Quercus borealis*, both ring porous trees like *Prosopis*, showed intense root growth in June-July and again in late August. Midsummer cessation of root growth is thought to be due to periods of drought or high soil temperature (Lyr and Hoffman, 1967). Significant rain occurred in early June which apparently translated into root growth in June and July with cessation of root growth by August. Hence, the low level of root carbohydrate in late June and early July appears to agree with existing literature. Reserve carbohydrates may be more available for root growth in trees with few flowers and pods, whereas, it would be later in the season before enough photosynthate is produced by the new leaves to satisfy above ground growth requirements of those trees with many reproductive organs (Wilson et al., 1974). After this second decline, the root carbohydrate concentration increased through July 26.

Influence of Bean Production

Trees sampled during June and July were grouped according to the number of pods actively growing on a tree. Trees which possessed an overall high reproductive potential and a relatively high proportion of pods had less reserve carbohydrates than did those trees which also had an overall high reproductive potential but possessed relatively few pods. However, the difference in reserve carbohydrates between the two groups decreased with each successive week.

During July, only maturing pods remained on the trees so the trees sampled had an abundance of pods or no reproductive organs. Root samples from trees which possessed maturing pods had an average TAC content of 11.1% while trees with no pods had an average TAC content of 19.8%. July 12 was the first sampling date in which the loss of green color in pods was noted. After July 5, root carbohydrates increased in trees possessing pods.

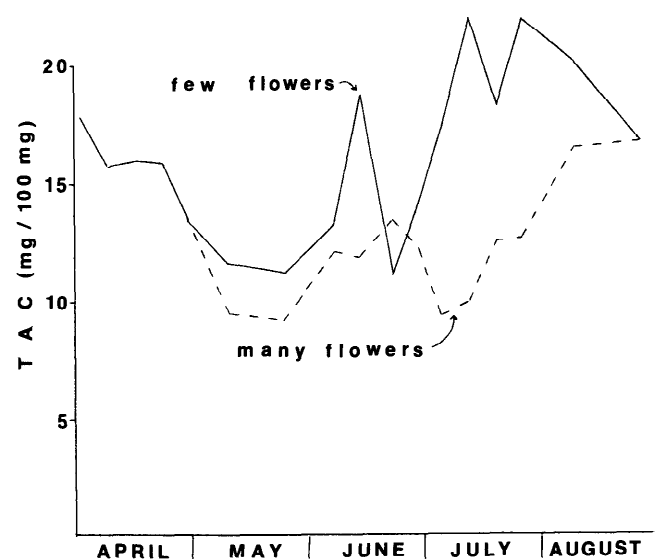


Fig. 3. Influence of relative proportions of reproductive organs on TAC concentration in honey mesquite roots.

Discussion

According to Dahl et al. (1971), soil temperature is probably the most important environmental factor influencing mesquite kill from 2,4,5-T during the optimum spraying season in West Texas, i.e., from mid-May through mid-June. They found that root kill of honey mesquite with 2,4,5-T was obtained only when the soil temperature at the 45 cm depth was at least 23.9°C during this period. The minimum root carbohydrate concentration of all trees sampled was recorded at approximately the same time that the soil at the 45 cm depth reached 23.9°C (Fig. 2). These results suggest that the net movement of carbohydrates from shoot to root tissue is indirectly related to soil temperature through its influence on root growth. Zimmermann and Brown (1971) reported that root elongation is correlated to the temperature on the root tips and not the temperature of the parent stem which would support this assumption. Hence, maximum 2,4,5-T translocation to root tissue in association with carbohydrates probably only occurs after the soil has warmed to the optimum temperature for root growth during early spring. However, factors other than soil temperature were more important in the latter part of June and early July. From the carbohydrate discharge and storage patterns found in our study, differences in physiological development due to relative proportions of reproductive organs (flowers and fruit) can explain the erratic herbicidal kills reported from herbicide applications made during late June and early July. Indications from this study are that stage of growth is equally important earlier in the growing season. However, it is impossible to tell the exact degree of stored carbohydrates from visual observations of phenological development. Figure 2 indicates that when soil temperatures reach 24°C, or above, mesquite trees growing on such sites have reached the stage in which net accumulation of root carbohydrates can occur and root kills from growth regulating herbicides are possible.

Changes in soil moisture were not reflected visibly in phenological development or in carbohydrate concentrations in the roots except possibly during June. It is generally believed that moist soil is necessary for active root growth. The soils of this study were dry during the early growing season (around 7% moisture by weight). Soil moisture increased to 11.4% during the first week in June (Fig. 2), which date coincided with the rapid replenishment of root carbohydrates and probably enhanced root growth during the mid- to late-June period. We assume that active root growth was responsible for the rapid depletion of root carbohydrates indicated in Figure 3 in late June.

Conclusions

Relating herbicidal control of honey mesquite to stage of growth, the following points are presented as the probable important events in effective control. Following bud burst and early spring growth, honey mesquite trees that had full-size mature leaves rapidly replenished the root tissue with carbohydrates (Fig. 3). Spraying with 2,4,5-T during this replenishment period should result in a good kill of trees with either many or few reproductive organs because of the net increase in root carbohydrates suggesting downward movement of the carbohydrates. Between June 22, 1971, and July 5, 1971, trees with a high reproductive potential showed a second decline in TAC while a second rapid increase in root carbohydrates occurred in trees possessing relatively few

flowers and pods. Herbicide application between June 22 and July 5 should give good kill of trees with a low reproductive potential. However, a poor kill of trees possessing many flowers and pods would probably result due to the loss of TAC during this time period. After July 5, trees of both phenological groups increased in root carbohydrates, a good time to spray, providing other conditions were favorable. This difference in carbohydrate recharge pattern largely explains the variation of mesquite susceptibility to 2,4,5-T during the latter half of the period commonly recommended (June 15 to July 15) for spraying mesquite in West Texas.

Although these results were obtained during only a 12-month period, they do provide a plausible explanation for the erratic mesquite root kills from foliar herbicide application in the Southwest.

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