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Multiple Effects of Precipitation on *Salix lasiolepis* and Populations of the Stem-Galling Sawfly, *Euura lasiolepis*

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Abstract

Relatively low winter precipitation (e.g., 18–28 cm from October to May compared to 45 to 65 cm) caused reduced growth of the arroyo willow, *Salix lasiolepis*, with number of shoots per stem initiated and shoot length reduced. Resources were reduced for the stem-galling sawfly, *Euura lasiolepis*, which declined in numbers after the relatively dry winter of 1980–81. Sawfly phenology was advanced relative to willow phenology in the 1981 generation, causing an additional reduction in resource availability. These direct effects of precipitation on the sawfly were increased by indirect effects on survivorship of the 1981 generation. Egg death in galls increased on water-stressed willow plants, forming the major mortality in the generation. This resulted in very low survival in the generation and an even lower population in the 1982 generation, even though resources recovered after high precipitation during the 1981–82 winter (46.7 cm). An experiment using high, medium, and low water treatments on potted willow plants demonstrated that the effects on willows and sawflies could be reproduced using only water as a variable.

Key words: *Euura lasiolepis*; Precipitation; *Salix lasiolepis*; Survivorship; Water experiment.

Introduction

Water availability to plants has been widely regarded as an important factor in the population dynamics of insect herbivores. The contrast between winter and summer rainfall was used by White (1969) as an index of stress on plants, and when extreme differences occurred between unusually high winter precipitation and unusually low summer precipitation, population outbreaks of psyllids on *Eucalyptus* were observed. This pattern was extended to other species of herbivores and to other forms of stress, but water stress remained a common apparent cause of insect outbreaks (White 1974, 1976). The postulated mechanism involves the indirect influence of water on nutritional quality of plant food. Rhoades (1979) extended this hypothesis by emphasizing the additional role of stress in changing plant defensive

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chemistry. In the four cases of water stress he cites, increases in defensive chemicals were observed. High water availability may also promote plant growth and increase resources for herbivores. This is what Davidson and Andrewartha (1948a, b) found in relation to *Thrips imaginis* in Adelaide, on the edge of the Great Victoria Desert.

Water also has direct effects on insect herbivores (Scriber and Slansky, 1981). As water content increases in foliage so growth rates of insects increase. Gradual declines in tree foliage water content are paralleled by reduced assimilation efficiency of herbivores. Water content in leaves is positively correlated with nitrogen content, so causes and effects are difficult to separate. However, Scriber and Slansky (1981) cite three studies in which water seems to have a major influence on herbivore growth rates.

Thus, insects on plants strongly influenced by water availability may well show dynamical properties associated with changes in the weather. Particularly, plants growing at the edge of a range determined by water supply may impose a strong influence on the population dynamics of their herbivores. At the low end of a water supply gradient unusually dry years will cause direct drought stress, while at the high end of the gradient unusually wet years may cause water logging and physiological drought, as White (1969) explains.

These considerations apply directly to willows (*Salix*) and their herbivores, for they are among the most water-demanding woody plants in many floras. Willows growing away from permanent bodies of water are likely to become stressed when precipitation is lower than normal. For this reason we have focused attention in our studies on herbivores of the arroyo willow, *Salix lasiolepis* Bentham, on the effects of precipitation on the plant-herbivore relationship. In Northern Arizona the arroyo willow usually grows in water courses with only temporary surface water, available during Spring melt of accumulated winter precipitation as snow.

Study Species and Sites

Salix lasiolepis in Northern Arizona grows as a shrub, 2–3 m in height. Many shoots grow from a central root stock, and vegetative spreading occurs by layering of stems, so one genet can spread over many square meters of ground by producing ramets. Each clone so produced is usually distinct from its neighbors, with differences in sex, stem and bud color, flowering and leafing phenology, and susceptibility to herbivores being common. Clones remain distinct physically also because, when clones abut, opposing branches support each other and layering in prevented. Therefore, clones can be distinguished and used as sampling units.

Most arroyo willow in the Flagstaff area of Northern Arizona, at about 2000 m above sea level, grows along Schultz Creek and the Rio de Flag which drain the San Francisco Peaks rising to about 4200 m. Winter precipitation as snow is usually abundant, and melt waters drain down these temporary streams.

We selected 16 willow clones for study situated along Schultz Creek which drains into the Rio de Flag, just north of Flagstaff (35°14'N, 111°30'W). Vegetation at this elevation is dominated by ponderosa pine, *Pinus ponderosa* Lawson, but the sides of the creek are occupied largely by arroyo willow which exists in pure stands. Seven willow clones were on Museum of Northern Arizona property (clones MNA 1 to 7) and the remaining nine clones were about 1 km below these, near Northland Press (clones NP 1 to 9). They were chosen to represent a wide range in phenological development and attack by herbivores. We preserve in this paper our original clone identification codes to enable easy cross reference among the many publications resulting from long-term studies.

The herbivore we concentrated on was a gall-forming sawfly, *Euura lasiolepis* Smith (Hymenoptera: Tenthredinidae). General life history, phenology, and mortality for a population in this area is described by Price and Craig (1984). The sawfly is specific to arroyo willow. It attacks young rapidly growing shoots of willow in May and June, forming a gall on early internodes. Eggs hatch in late June to early July. Larvae complete feeding in November and December, spin a cocoon in the gall, and overwinter. Adults emerge from galls in the following May and June to complete the life cycle. The sawfly is univoltine, and we designate generations by the year in which galls are initiated.

An experiment using potted willow plants was located at Coyote Spring, on Museum of Northern Arizona property, within 1 km of all wild clones studied. The spring supplied water for the potted plants throughout the summer of 1983. Two willow clones at the spring supported high densities of sawflies so that attack of potted plants by naturally occurring sawflies could be studied.

Methods

Patterns in willow growth on the 16 clones were sampled in 1980, 1981 and 1982. Vegetative growth was sampled on each clone at 7 day intervals early in the season, and as rate of growth declined sampling frequency was reduced to about once per 14 days. For each clone 3 branches, and five stems which grew in the previous year per branch were haphazardly selected. On these, new growth was measured, recording the number of vegetative buds developing per stem, measuring the length of the longest shoot per stem, and counting the number of leaves present on all shoots per stem. Since sawflies oviposit into the young shoot through the bases of petioles, leaf number provides an estimate of resource availability. The longest shoot per stem was measured because sawflies attack long shoots more frequently than short shoots so the longest shoots provide the best index of resource availability (Craig et al. 1986).

Sawfly attack was monitored each year when willow growth was studied, by counting oviposition scars in petioles, so the number of attacks per shoot could be estimated. The number of galls formed per shoot was used as an estimate of sawfly population size for that generation. For 1983 and 1984 generation sawfly density estimates were made on clones MNA 1–7 and NP 4, 5, 7–9 by repeatedly throwing a line over a clone and counting the number of galls per shoot on shoots within 30 cm of the line, until a total of 1000 shoots per clone were sampled.

Sawfly survivorship curves were developed for each generation by collecting at least 100 galls after cocoons had been spun, from some clones with high populations (e.g., MNA 2 and NP 8). Galls were opened and the following recorded: number of living sawflies, time of death as egg, early, mid or late larva, according to larval size, and where possible causes of death from parasitoids or predators. Each survivorship curve is presented as percent surviving of the cohort in relation to the stages of development: 1 = egg, 2 = early larva, 3 = mid larva, 4 = late larva, and 5 = larva in cocoon. Calender time for these stages is provided in Price and Craig (1984).

Precipitation per month was obtained from local weather records observed and recorded by a U.S. National Oceanic and Atmospheric Administration (NOAA) station at Flagstaff (Pulliam) airport, about 11 km from the study sites. A private weather station operated by Dr. Charles Heaton about 1.5 km from the study sites provided data that was strongly correlated with NOAA data ($Y = 3.84+0.86X$, $n = 6$, $r^2 = 0.97$, $p<.01$). This correlation was based on October to May precipitation for the winters 1978–79 to 1983–84. We feel, therefore, that the NOAA station record is representative of our study sites and we used these, as they are published and available to the public (National Oceanic and Atmospheric Administration 1984a, 1984b).

An experiment was conducted to test for direct effects of water supply on willow growth, gall growth, and sawfly attack and survival. From each of the clones MNA 1 and 2 and NP 8 and 9, nine cuttings of juvenile shoots were rooted in sand in 1982. One plant of each clone was then planted in one 19 litre pot containing a mixture of alluvial sandy silt from the MNA and NP sites in which the original clones grow. The nine pots were then assigned in 1983 to water treatments at random, three pots per treatment. The high water treatment (HW) involved saturating each pot with water every day until water ran from the bottom of the pot and was retained in a pan 4 cm deep and 30 cm diameter. The medium water treatment (MW) involved the same treatment once per 7 days. The low water treatment (LW) involved watering as in the other treatments, but 22 days apart initially (May 28 and June 19), and then at 14 day intervals. All treatments were applied from May 28 to October 10, 1983, and after this time water was applied as needed. No fertilizer or other chemicals were applied to plants or soil at any time during 1982 and 1983.

Measurments on all potted plants were taken as follows in 1983. When oviposition was completed the number of attacks per plant was counted on July 6. The number of shoots per plant was counted and the length of the 10 most distal shoots measured. All galls were collected from all plants on December 1, their greatest width was measured and wet weight was taken. Galls were then opened and the contents recorded as in the sawfly survivorship studies on the wild clones. In addition, live larvae were weighed on an electro-balance. By December some shoots with galls had abscised, although living sawflies remained in some of the galls. These were included in the analysis.

Statistical analysis employed standard methods of one-way analysis of variance, and the least squares method of linear regression (e.g., Snedecor 1956). Analyses using data collected from willow clones and potted plants were all based on mean values per plant. This avoided the use of multiple samples per plant which were thus not independent of each other (pseudoreplication is avoided). Analysis of variance between two samples established whether significant differences existed.

Results

The pattern of precipitation in the Flagstaff area includes winter precipitation, most of it as snow, and summer rains from early July into September (Fig. 1). June is usually a very dry month. This is the month of strong willow growth, sawfly attack and the time when eggs are in the newly formed galls. Thus, if growth of willow is influenced by precipitation it must be that which falls in winter. The summer rains may start to have an influence on growth by mid July but this is about 8 weeks into the growing season for willow and after the critical egg stage of the sawfly. Therefore we use winter precipitation, from October through May, as an index of water availability to willows in the following season. NOAA records show that winter precipitation was as follows for the years of our study: 1978–79, 61.9 cm; 79–80, 64.6 cm; 80–81, 27.8 cm; 81–82, 46.7 cm; 82–83, 53.3 cm; 83–84, 18.1 cm. The winters of 80–81 and 83–84 proved to be unusually low in precipitation with less than 50% of the precipitation measured in the 78–79 and 79–80 seasons.

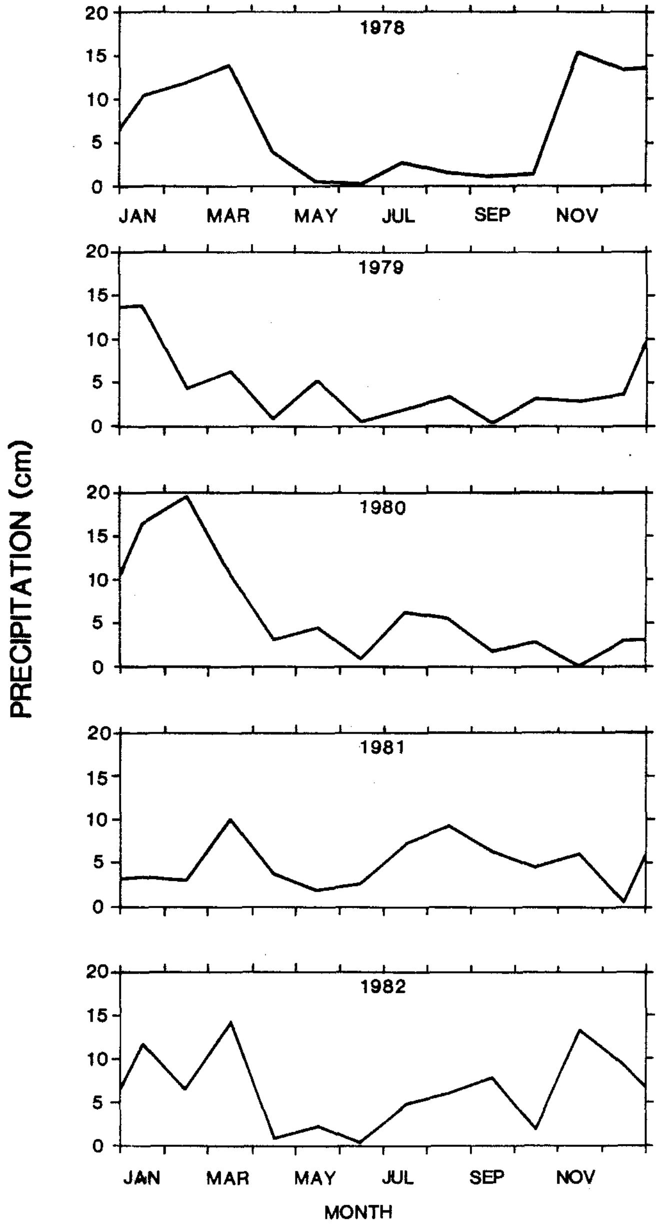

Fig. 1. Monthly total precipitation (cm) at Pulliam Airport, Flagstaff, for the years 1978 to 1982. All values are rain equivalents although most precipitation from November through April is in the form of snow. Note that June is usually one of the dryest months of the year, and that the winter of 1980–81 had relatively low precipitation.

Response of the 16 wild clones of willow to the low precipitation of 80–81 was a significantly reduced number of shoots produced per stem, and a significantly reduced shoot length (Fig. 2). Since the number of leaves that can act as oviposition sites for sawflies increases with number of shoots and shoot length, a resource index derived from the product of these two

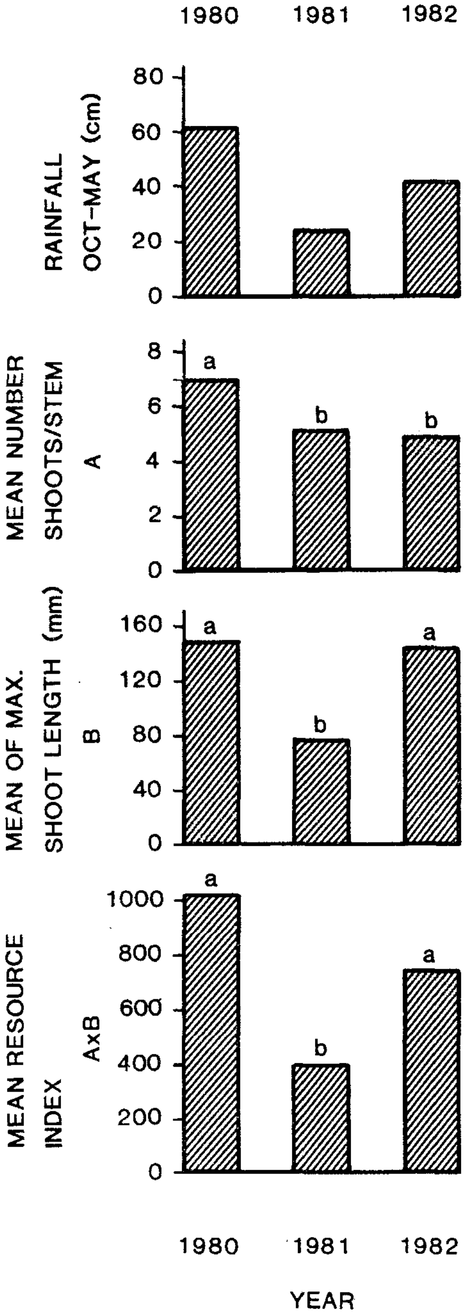

Fig. 2. Data on winter rainfall, mean number of shoots per stem (A), mean of maximum shoot length per stem (B), and mean resource index (A × B). Histograms represent means of 16 willow clones, MNA 1–7 and NP 1–9, for the years 1980, 1981, and 1982. Letters above columns, when the same, indicate no significant difference between means ($p > .05$) and when different indicate significant differences ($p < .05$).

estimates was calculated (Fig. 2). This index declined significantly, being over 2.5 times smaller after the drier winter. Resources became much less abundant for the 1981 generation of sawflies.

After the winter of 81–82 with more precipitation than in 80–81, the willows grew better, producing shoot lengths not significantly shorter than in 1980. The number of shoots initiated per stem was still depressed, probably because shorter shoots in 1981 produced fewer vegeta-

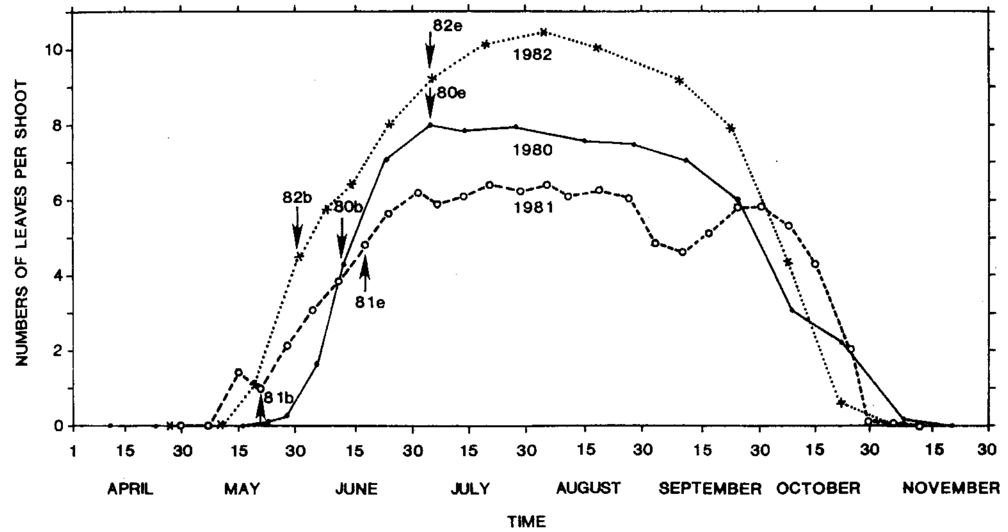

Fig. 3. Phenology of leaf production and sawfly attack on clone MNA 2 as an example of differences in phenology in the years 1980, 1981, and 1982. Arrows indicate times of first and last observations on new ovipositions in each year. Each arrow is labelled with the relevant year, and b for beginning of oviposition, and e for end of ovipositon. Mean production of leaves per shoot over the oviposition periods were 0.16 leaves per day in 1980, 0.14 in 1981, and 0.14 in 1982.

tive buds for the 1982 season. However, the resource index for 1982 increased to a level significantly greater than for 1981, and not significantly different from that for 1980. Because growth was depressed in the 1981 season we are justified in claiming that willows were more stressed in 1981 than in the seasons 1980 and 1982, resulting from low winter precipitation.

Weather differences between these years also influenced the phenology of willow shoot development. Production of leaves in 1981 was over 10 days in advance of the 1980 season during May, and then rapidly fell behind 1980 production in June as the effects of water shortage increased (Fig. 3). In 1982 growth was also relatively early and for the smaller number of shoots produced, growth was stronger than in either of the preceeding years. The early effects of precipitation on phenology were probably indirect, for accumulated snow would cool temperatures and bury branches, and delay phenology in this way.

Sawfly densities declined strongly from the 1980 generation to the 1981 generation (Fig. 4).

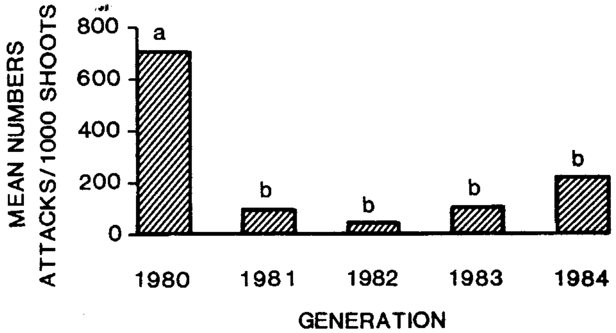

Fig. 4. Mean number of sawfly galls per 1000 shoots for all clones censused from 1980 to 1984. Letters above columns are as in Fig. 2.

The population continued to decline in the 1982 generation, and a recovery has been evident in 1983 and 1984 with populations doubling from 82–83 and 83–84. There appears to be an immediate effect of reduced willow growth on sawfly density, the mechanism being reduced resource availability.

Change in relative phenologies of willow and sawfly probably also contribute to the

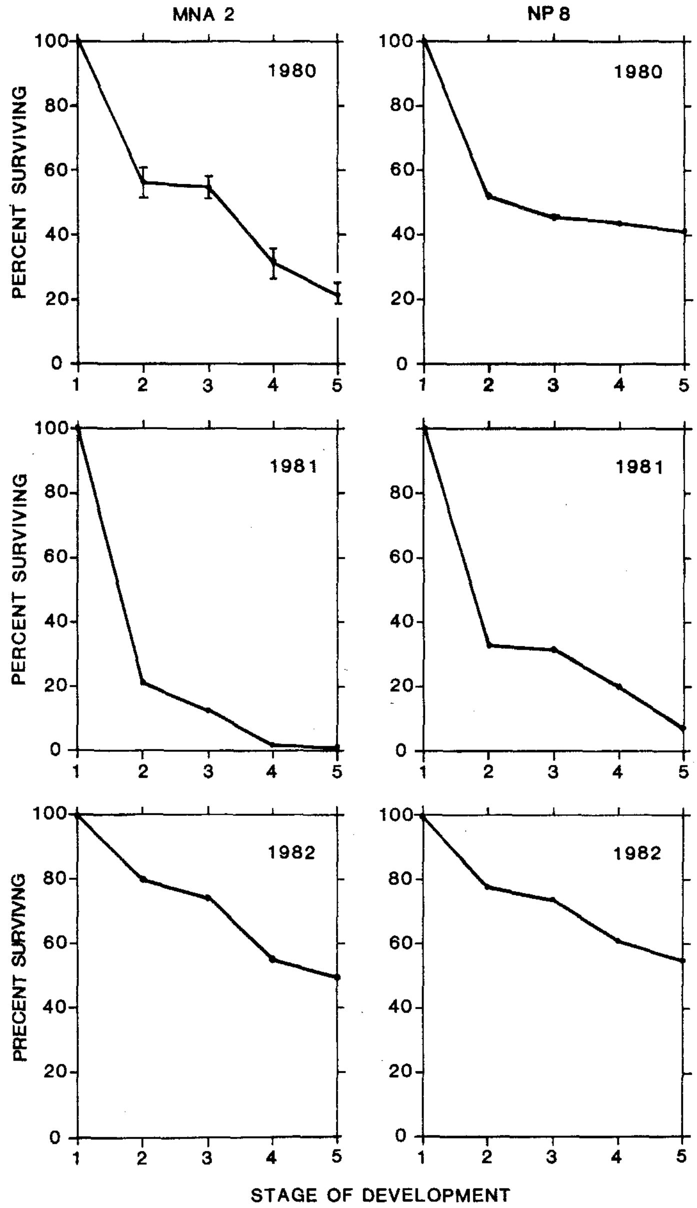

Fig. 5. Survivorship curves for sawflies on clones MNA 2 and NP 8 for the years 1980, 1981, and 1982. In 1980 three replicate samples were taken on MNA 2 and the mean and range in these samples is shown indicating the small variation to be expected between samples. Stages of development are 1. egg; 2. early larva; 3. mid larva; 4. late larva; 5. larva in cocoon. Note the increased egg death in 1981 in both clones and then the reduced egg death in 1982.

immediate, rapid decline in population after a dry winter (Fig. 3). In 1980 and 1982 attack by sawflies was first recorded on June 12 and May 31 respectively. In both years shoots had a mean of five leaves and leaf production was more rapid than at any other time of the year. In both years no ovipositions were observed after July 5, ending as leaf production slowed. In 1981, the pattern changed and attack was much earlier, first observed on May 20. At this time there was a mean of only 1 leaf per shoot. It appears that sawfly phenology is advanced much more than willow phenology after a dry winter, and some sawflies emerge before resources are sufficiently developed for all females to lay the majority of their eggs. With females living for only a mean of 4.6 days (Price and Craig 1984) those emerging early may compete severely for the small number of shoots long enough for oviposition, and die before resources become more abundant. In 1981 oviposition ended by June 18, 17 days before the time in 1980 and 1982. We have not established that shortage of resources and competition through phenological changes are important as mechanisms, but the evidence is strongly suggestive that an immediate effect of low precipitation works in this way.

Survivorship curves for the 1980, 1981 and 1982 generations show that there was also a delayed effect on sawfly density. Curves for two clones with usually high sawfly densities, MNA 2 and NP 8 show dramatic changes between years (Fig. 5). Survival to larvae in cocoons (5th stage of development) on MNA 2 was as follows: 1980, 22 %; 1981, 0.5 %; 1982, 50 %. Survival on NP 8 showed a similar pattern: 41 %, 7 %, 56 %. Much of this change in survival was accounted for by death of eggs. Survival on MNA 2 to early larvae (2nd stage of development) for the three years was 57 %, 21 % and 80 %, and on NP 8 it was 52 %, 33 % and 78 %. Water stress on willows appears to have a strong effect on egg death during June.

The relationship between winter precipitation and egg death was tested using data from six sawfly generations on MNA 2 for which we have survivorship data (the 1979 to 1984 generations). The two generations occurring after unusually dry winters had exceptionally high egg death (1981 and 1984 generations) (Fig. 6). The relationship over the six generations showed a clear negative trend, but it was not significant although winter precipitation accounted for 55 % of the variance in percent of eggs dying in a cohort ($n = 6, r^2 = 0.55, .10 > p > .05$).

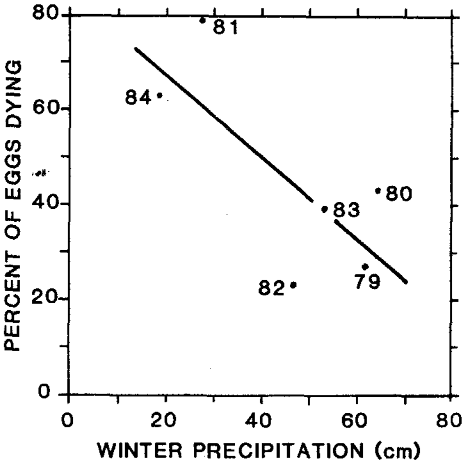

Fig. 6. Regression of percent eggs dying on winter precipitation (cm) in MNA 2 for generations 1979–1984. Data points are labelled according to generation. The regression equation is $Y = 84.39 - 0.85 \times X$ ($n = 6, r^2 = 0.55, .10 > p > .05$).

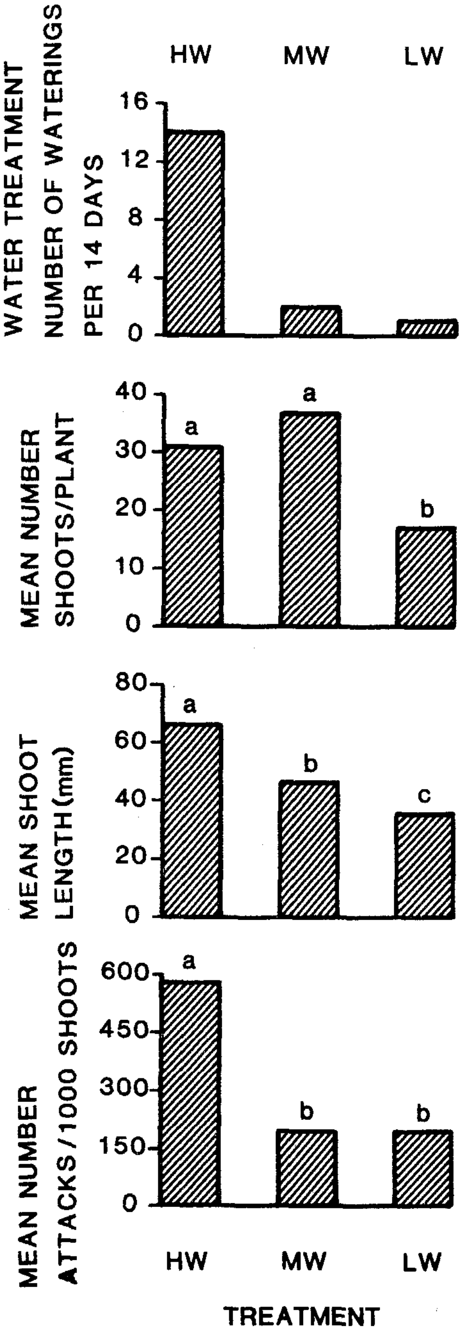

Fig. 7. Results from water treatment experiment for high water (HW), medium water (MW), and low water (LW) treatments. Letters above columns are as in Fig. 2.

The direct effects of water availability without the possible complications of other factors was tested with the water treatment experiment. There was a significant reduction in the number of shoots developed per plant in the low water treatment (Fig. 7). Also, there were significant reductions in the mean shoot lengths in the medium and low water treatments. These growth differences had an immediate and direct effect on the number of sawfly attacks, with attacks on medium and low water treatments being three times lower than on the high water treatment. These results simulated closely the effects of water on willow growth in the field observed in 1980 and 1981. Water availability has a direct effect on willow growth and provision of resources for sawflies, and the number of attacks made by sawflies.

The differences in levels of attack by sawflies on experimental plants persisted through the immature stages of the sawflies. The mean number of eggs per plant, early larvae per plant, and larvae in cocoons per plant showed significant differences between treatments (Fig. 8). However, surviving larvae in cocoons were not significantly different in weight, and gall diameter and weight were not significantly different (Fig. 9).

Survivorship curves for sawflies on the three water treatments showed very little or no mortality after the egg stage (Fig. 8). The only large difference in the curves resulted from differences in egg death, which increased as plants were more water stressed, from 24% dying in the high water treatment, to 32% dying in the medium water treatment, and 61% dying in the low water treatment. These differences represent much of the range in egg death on wild willow clones, indicating that water availability has a pure indirect effect on egg survival. No death of larvae resulting from parasitoid attack or predation was observed. The survivorship curve and the evidence that larval weights do not differ between water treatments (Fig. 9) indicate that water stress has no effect on sawfly development once larvae have hatched from the egg.

Discussion

The mechanisms causing population change of the stem-galling sawfly influenced by winter precipitation are both direct and indirect. We have demonstrated a direct and immediate impact on willow growth involving reduction in number of shoots and length of shoots, and an overall reduction in the resources available to sawflies. We have also suggested a direct

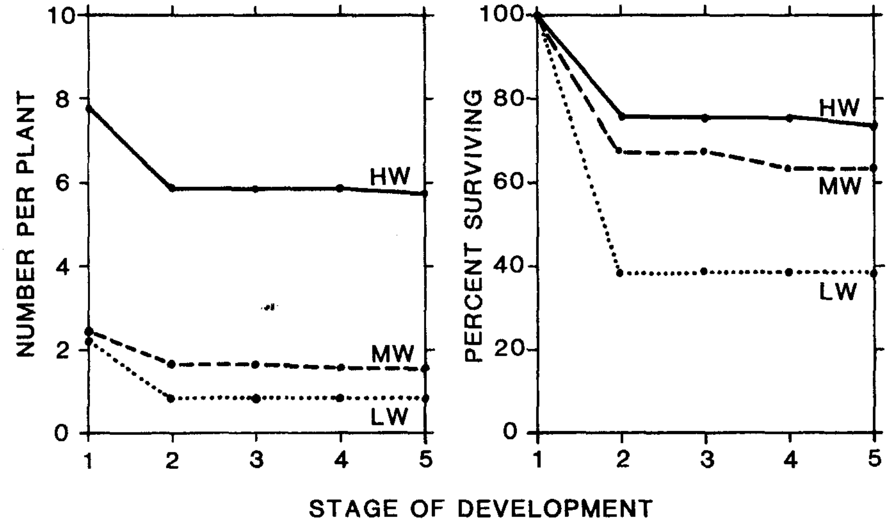

Fig. 8. Survivorship curves for cohorts of sawflies in the water treatment experiment. Treatments are denoted as high water (HW), medium water (MW), and low water (LW). Left: values are per plant; right: values are percent surviving per cohort. Stages of development are as in Fig. 5. The significant differences between HW and LW treatments in mean number of attacks/1000 shoots (Fig. 7) persist throughout the development of the sawfly. After the egg stage the MW treatment is not significantly different from HW or LW treatments.

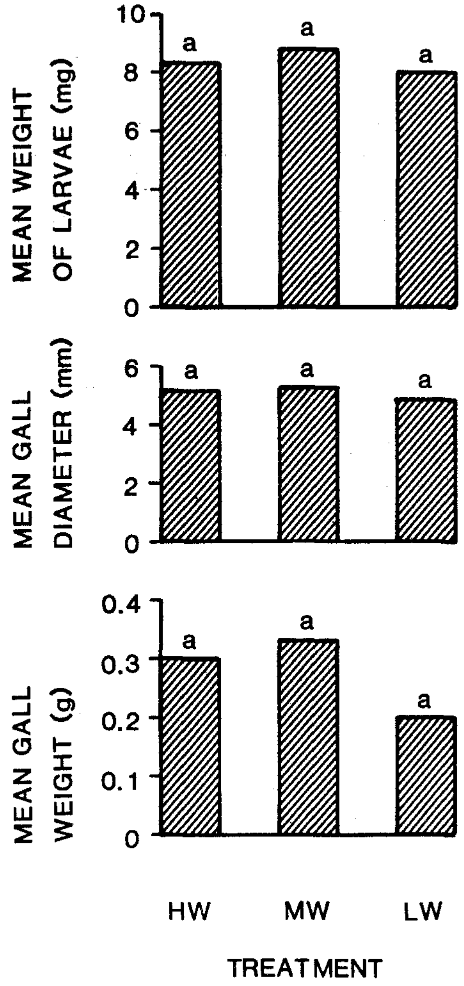

Fig. 9. Results from water treatment experiment for high water (HW), medium water (MW), and low water (LW) treatments. Letters above columns are as in Fig. 2.

and immediate effect on the next sawfly generation by changing the relative phenologies of willow and sawfly such that there is a probable shortage of oviposition sites early in the season. These effects are additive and caused a dramatic decline in sawfly numbers following a relatively dry winter in 1980–81. The indirect and delayed effect of low winter precipitation worked through a change in willow quality such that eggs died in galls with much higher frequency. Egg death was the major mortality factor and was largely responsible for very low survivorship to the cocooned larval stage. Hence, the adult population from the 1981 generation was very small, few eggs were laid, and the population showed a continued decline into the 1982 generation, even though resources recovered in 1982. The direct-immediate, and indirect-delayed effects of winter precipitation are cumulative and over three generations, 1980 to 1982, caused a very strong decline in population of over 14 fold (Fig. 4).

The same immediate effect of a relatively dry winter was not recorded in the 1984 generation. Detailed growth and phenology studies were not undertaken in 1984 so comparisons are not possible on the direct effects. The indirect effects are evident in the high egg death in the 1984 generation (Fig. 6) which will probably cause a population decline in 1985. Experimental results also showed a direct and immediate effect on willow growth and sawfly attack (Fig. 7), as well as the indirect and delayed effect (Fig. 9), supporting our conclusions based on field studies. The population increase after a drier winter in 1983–84 therefore remains unexplained.

The mechanisms causing increased egg death in galls after dry winters are being studied now. Eggs of sawflies usually absorb water from plant tissues during embryogenesis as do those of *E. lasiolepis* (Price and Craig, 1984). During dry periods galls may contain reduced water, cell contents may have a higher osmotic potential and reduce water availability to sawfly eggs, causing their death. If this hypothesis is correct, a largely physical phenomenon will define change in plant quality for this sawfly, or plant resistance. The large differences in egg death from generation to generation described in this study support White's (1969, 1974, 1976) contention that early stages of herbivorous insects are critical in population dynamics and deserve more detailed study.

Differences between survivorship curves on natural willows and experimental willows are apparent. In the field mortality continues after egg death (Fig. 5) whereas in the experiments the only major mortality was egg death. One major difference is that parasitoids did not attack sawflies on experimental plants but they caused the majority of mortality recorded between developmental stages 3 and 4 on sawflies on the native clones. Chickadee predation also accounted for death of larvae in cocoons on wild plants, but galls on experimental plants were removed before such predation occurred. The remainder of the differences result from unexplained death of larvae on wild plants and very little on the experimental plants.

This study demonstrates that plants stressed after low winter precipitation provide poor resources for a major herbivore, both in terms of resource quality and quantity. These results contrast with arguments by White (1969, 1974, 1976) and others (e.g., Rhoades 1983) that stressed plants are favorable for insect herbivore population increase. The generalizations by White and Rhoades do not apply to all insects. For example, aphids suffer detrimental effects on continuously stressed plants, and effects of stress depend on the balance between detrimental effects of lowered phloem pressure, a physical factor, and beneficial effects of increased soluble nitrogen following hydrolysis of proteins in leaves, a chemical factor (Wearing, 1967, 1972). Thus the term stress is totally inadequate as a descriptor of plant condition, and generalizations will not be possible for any group of animals unless stress is described in terms of the physical and chemical needs of the organisms under study. Our study on *E. lasiolepis* shows that stressed plants have immediate and delayed negative effects on herbivore populations.

The developing theory on plant-herbivore interactions (e.g., Rhoades 1983) emphasizes qualitative changes in plant chemistry following stress that benefit herbivores without considering quantitative changes in resource availability that play a major role in the *E. lasiolepis* system. The emphasis on chemical plant properties also fails in the perception of physical properties being important, and perhaps equally important. In related studies on *E. lasiolepis*, in relation to changes in nutrition, chemical defense and vigor of plants only plant vigor (measured as mean shoot length per plant) was a persistently good predictor of sawfly attack and survival (Waring et al. 1986). While all physical plant characteristics have a chemical basis, at present for *E. lasiolepis* it appears that largely physical plant properties determine success of the sawfly. We suggest that more emphasis in insect herbivore-plant studies in defining stress in terms of quantitative and qualitative changes in both physical and chemical properties relative to herbivore requirements will be rewarding.

Acknowledgments

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