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Title: WATER RELATIONS OF 'OLYMPUS' STRAWBERRY AND THE GROWTH RESPONSE TO DRIP IRRIGATION AND POLYETHYLENE MULCH

Abstract Approved:
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A series of field experiments were designed to determine the plant growth and yield responses of strawberry (*Fragaria* x *ananassa* Duch. cv. Olympus) to three rates of summer drip irrigation, with or without black polyethylene mulch. Additional field, greenhouse, and growth chamber studies sought to identify some of the physiological bases for reduced vegetative growth in response to water deficit. The relationships between leaf water status and both stomatal behavior and leaf elongation were characterized.

Field plantings for the irrigation trial were established in May of 1977 and 1978 and received differential irrigation (0, 0.23, or 0.70 of pan evaporation) during midsummer for one month in 1977 and two months in 1978. During the driest portion of each year the water potential of the sandy loam soil at 20 cm depth remained above -0.3 bars for the highest irrigation rate with mulch, and fell below -11 bars at the lowest rate without mulch. Vegetative growth was significantly increased by both irrigation and mulch. Crowns, leaves, and stolons

(runners) were counted monthly, and leaf area and dry weight of leaves, crowns, and roots were determined the following July after fruit harvest. The growth enhancement due to irrigation and mulch was strongly partitioned to top growth rather than roots. Among two year old plants those in the mulched and more highly irrigated treatments had a very large number of leaves and crowns (up to 223 and 26, respectively), yet the leaf area averaged 27% lower than that of one year old plants. The number of flowers in the first crop year was increased by irrigation in both plantings but was only increased by mulch in 1977. The number of harvested fruit was increased by irrigation in 1977 and by mulch in 1978. The effects of environment (including frost damage one year) on yield component relationships were discussed. Irrigation and mulch each caused a significant increase in fruit yield in one of the two years. No yield response to treatments occurred in the second year crop of the 1977 planting, although it received a second season of treatment which caused large differences in plant size. In general, fruit yield responded more to mulch than to increased summer irrigation. Mulch also increased the relative water use efficiency.

Stomatal behavior in 5-month-old irrigated (IR) plants was compared to that in plants which were non-irrigated (NIR) for up to 36 days. Minimum leaf water potential (ψ) in both IR and NIR plants often reached -16 bars in the field, but never fell below that level even with pan evaporation rates up to 1.42 cm per day. ψ in IR plants was only higher than in NIR plants when evaporative demand was lowered due to cloudiness, and turgor (ψ_p) was similar even when the treatments differed in ψ. However, leaf conductance (K_ℓ) rates in NIR plants were half or less those in IR plants both during the day and night.

Light level and soil volume were both lower for plants in the greenhouse and growth chamber compared to field plants. The combined effect of the two factors was that in the indoor environments, ψ in NIR plants was several bars lower than in IR plants. Low light flux (250 $\mu E\ m^{-2}s^{-1}$) in the growth chamber also affected stomata directly, reducing K_{ℓ} compared to field rates over a wide range of leaf ψ. Osmotic adjustment occurred to a moderate degree (ψ_s of NIR plants was decreased 2-3 bars more than the amount expected due to dehydration), but it was inhibited by light flux densities below 500-800 $\mu E\ m^{-2}s^{-1}$.

The relationship of leaf elongation (which was proportional to increased area) to ψ_p was examined in two environments. In the greenhouse a positive influence of increasing ψ_p on elongation was observed, while in the field the inhibitory effect of low temperature was apparent during the night, so that no straightforward relationship between ψ_p and elongation could be established. A growth chamber study found that the optimum temperature for leaf lamina elongation was between 22° and 28°C. Petiole elongation had a higher optimum. In a 14-day field study the daily rate of elongation was higher and the final leaflet area was 85% greater in IR plants. Approximately half of the daily leaf expansion occurred during a three to five hour period in the evening. The underlying causes of the large reduction in vegetative growth in water-deficient strawberries can only be inferred at this time. While reduced elongation corresponded to reduced ψ_p in the greenhouse, this was not observed in the field. Either very small reductions in

ψ_p in NIR field plants caused large reductions in leaf elongation, or facets of water deficit other than ψ_p level were responsible. The greenhouse result may be considered artificial, since osmotic adjustment was absent.

WATER RELATIONS OF 'OLYMPUS' STRAWBERRY AND THE GROWTH RESPONSE TO DRIP IRRIGATION AND POLYETHYLENE MULCH

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WATER RELATIONS OF 'OLYMPUS' STRAWBERRY AND THE GROWTH RESPONSE TO DRIP IRRIGATION AND POLYETHYLENE MULCH

INTRODUCTION

Water deficiency is the most important factor limiting crop yields world-wide (21). In less developed countries increased food production cannot be assured by reliance on rainfall, and water for irrigation is often scarce. Increased demands on water resources for irrigation and other uses in industrialized countries have depleted aquifer reserves, raising the propsect of reduced access to irrigation water. Continued development of water resources for agriculture is also likely to encounter more constraints due to economic, environmental, and recreational considerations. Horticultural crops often have a high water content and large irrigation requirements. Premium production areas, where water is plentiful and the climate is either temperate in the summer or warm in the winter, are also attractive to people and industry. Rapid population growth may require that horticultural producers either sustain high yields with less water or relocate (to areas with less water).

The challenge to agricultural research can be responded to along two avenues. One is to develop irrigation delivery systems and cultural practices which allow more efficient use of available water. Secondly, crop plants will need to be modified for increased water use efficiency (WUE = yield/total water use), or to allow adaptation to cropping areas with less available water or greater evaporative demand. This will require greater knowledge of the water relations physiology, which is particularly scarce for horticultural crops. Characterizing plant responses to water deficit should identify mechanisms which favor higher WUE or which result in desiccation avoidance by plants. It may be possible to incorporate these into new cultivars, adapting them to the water supply and environment of the different growing regions.

Strawberry cultivars often require a high level of soil moisture to maintain maximal growth (167) and fruit yield (8), therefore irrigation is practiced in most production areas. Polyethylene mulch is also commonly used as a production aid in California. A planting of the 'Olympus' cultivar, grown with drip irrigation and black polyethylene mulch, produced five times the average yield in Oregon (131). This raised questions concerning both the water conserving capabilities of the mulch and drip irrigation and the cause of the high yields. Were the high yields a result of the plant structure of 'Olympus' (which may be conducive to enhancement by the cultural system), or were they due to physiological changes of a water relations nature? Very little is known about strawberry water relations.

The objectives of the crop response studies are 1) to evaluate the vegetative and reproductive growth responses of 'Olympus' strawberry to mulch and increased rates of irrigation, and 2) to determine if the relative WUE of 'Olympus' is greater with polyethylene mulch. The objectives of the leaf water relations studies are 1) to characterize stomatal behavior in strawberries with high or low soil moisture and relate the behavior to leaf water status and light level, and 2) to compare the leaf elongation rates of plants with high and low soil moisture and describe the influences of leaf turgor and temperature on elongation.

REVIEW OF LITERATURE

Strawberry Morphology and Yield Components

Stolon Formation and Crown Branching

A strawberry plant consists of one or more somewhat independent structures called crowns, each of which can produce adventitious roots, leaves, stolons (runners), branch crowns, and inflorescences. Leaf initials are born spirally and the terminal growing point completes its development as an inflorescence. Extension growth, which is sympodial, is continued by the uppermost axillary bud (166). A bud may develop into a stolon or branch crown, with differentiation determined by genotype and the growth environment. The time during which buds cease to differentiate into stolons and instead become branch crown buds is determined by the photoperiod and is often associated with the time of inflorescence formation on a crown (80). Cultivar variability with respect to this factor leads to important differences in plant structure.

Flower Initiation

The single cropping strawberry is a facultative short day plant. Flowering is thought to be inhibited by long days, as opposed to being promoted by short days. Guttridge postulated the presence of a hormone which promotes vegetative growth and inhibits inflorescence initiation (81, 82). Mature leaves are more inhibitory than young leaves in this respect (194). The effect of leaf removal on floral initiation was studied, and cultivar differences were detected (84). The presence of fruit on a plant in June can induce initiation during non-inductive long days in cultivars with weak photoperiodic control (132). Conversely, high temperature or excess vigor can reduce initiation in these cultivars during usually inductive short days. It has long been known that temperature and photoperiod interact in strawberry, and the relative importance of the two factors in controlling initiation varies with cultivar (62). Recently Heide (88) studied the interaction in controlled environments, and grouped cultivars into two categories according to their floral initiation responses: weakly photoperiodic cultivars (early fruiting cultivars, often used in marginal growing areas at high north latitude), and more standard cultivars. Vegetative growth and flowering showed generally opposite responses to the environmental variables, but were to some extent independent, which casts some doubt on the single hormone hypothesis of floral initiation control.

Leaf Growth

Abbott (1) found that, in contrast to an earlier conclusion (11), cell division and cell expansion proceed concurrently in strawberry leaves. Each leaf subtends a bud, which contains the primordia of the next four to six leaves. The interval between emergence of leaves was six to eight days in the study of Abbott, and final leaf size was determined mostly by the duration of cell expansion in the late stages of leaf growth, and not by the duration of cell division in the pre-emergent period. The rate of leaf production for an English cultivar was found to be maximum in June, but also high in July and August (10). Leaves developing in late summer have a reduced final size, probably due to photoperiodic control of the cell expansion process (1, 12).

Root Growth

Adventitious roots are present on a crown when it is planted, and new ones rapidly develop, but are devoid of root hairs. Branching occurs and on this framework develops a transient system of fibrous roots, which are the true absorptive organs (127). In potted plants low soil moisture was found to reduce the number and dry weight of roots, but root length and lateral growth were increased (52). In another pot study the root mass was inversely correlated to fruit load, with total dry matter in the plant fairly constant (117).

Yield Components

The fruit yield of a strawberry plant is considered a function of the number of crowns per plant, the number of inflorescences per crown, the number of flowers per inflorescence, the percentage of flowers that develop into fruit, and the fruit size. Yield is usually closely correlated with the number of fruit, and may or may not be strongly associated with the number of inflorescences (83, 95). The number of inflorescences per crown is a function of cultivar and environment. If nearly every crown has an inflorescence then the number of crowns becomes a primary yield factor. The number and area of leaves is closely related to number of crowns, and plant size (height times width) is a function of all of these. The relationship of fruit yield to plant size or leaf area varies with cultivar, as well as latitude (85, 114, 149, 187, 206). Yield increases with plant size, unless plants are grown with excessive fertilization (38) or at a high latitude (85). Plant age is also a factor since the number of crowns per plant increases with time (25, 36, 27). However, the relationship of crowns to leaf area or root mass may change with time, so that fruit yield does not always increase with age (149).

Fruit size is determined primarily by the number of achenes, which varies with genotype and is closely related to the position of the flower within the inflorescence (217). This has been considered a form of apical dominance, since removal of the primary fruit increases the size of the secondary fruits, but the reverse does not hold (98, 170, 189). The surface area per achene has been adopted as a measure of fruit enlargement relative to the full potential to account for environmental influences (2, 216, 217). These workers examined inflorescence morphology (pedicel and peduncle diameter) in terms of water transport capacity, and considered it to be capable of limiting fruit to less than their full size potential (215). Fruit size is usually reduced as a strawberry planting ages. In Norway this was found to be a result of both a decrease in the number of achenes per flower and the receptable enlargement per achene (36, 37).

Another environmental factor that affects several yield components is temperature (122). This is noteworthy in that mulching, which is a common practice in some areas, can alter soil and leaf temperatures appreciably.

Strawberry Growth Response to Cultural Practices

Response to Irrigation

A review by Salter and Goode concluded that strawberry growth and fruit yield in several environments can be increased by irrigation (171). During the establishment of newly planted crowns soil moisture is essential for rapid root development. Preliminary work found that strawberry growth was maximized by keeping soil water potential above -1.0 bars (167). It is generally recommended that plantings be kept well watered throughout the first season (54, 68, 169, 173). Irrigation during the first summer results in the maximum number of stolons and rooted runner plants (146, 207). It also gives the greatest leaf and crown growth of the mother plants or runner plants, depending on the cultural system used (147, 169, 203). The rate of leaf production can be reduced by drought, but restored within a few days by irrigation (10).

The effects of July and August irrigation on fruit production the following spring are not clearcut, however. Increased vegetative growth is not always followed by increased yield (23), or even by an increased number of flowers (169). In an Arkansas study (203) irrigation during the first season gave 33-51% higher yield; but the results were ascribed mostly to an increased number of plants per acre due to better filling in of the rows with runner plants. However, frequent applications of water yielded no better than the drier regime with only three or four irrigations per season. In fact, a detailed study in Oregon showed that frequent irrigation can result in an overproduction of rooted runner plants and a fruit crop which is inferior to that from rows in which plants were thinned (207). Work in England suggested that maximum runnering did result in the highest fruit yield (8).

Some of the ambiguity concerning the yield response to midsummer irrigation may be due to effects on floral initiation, which are only poorly understood. Using potted plants maintained at a moderately low average soil moisture (irrigated at 20% of available soil water), Naumann (146, 147) compared the effects of high soil moisture during each consecutive four week interval throughout the first season. He found that high moisture in June (3 months after planting) and in August reduced the fruit number and yield. He drew on Guttridge's hypothesis of a floral inhibitor in mature leaves to explain the June effect, since it caused the highest fresh weight of mature leaves to be present in early September, when initiation commences. Irrigation just prior to initiation time also delayed its onset, and therefore reduced its duration since initiation ceases and plants become dormant in response to low temperature, without regard to when it began (25, 147). The reverse approach, withholding water during each of five consecutive 30 day intervals, produced supporting results (112). Withholding water in August resulted in the highest number of fruit and yield. Unfortunately, a treatment was not included in which irrigation was provided through all five intervals. The cultivar variation in strength of photoperiodic control of floral initiation, discussed previously, may require specialized irrigation practices. It has been suggested that in the southern USSR to avoid autumn flowering of early and midseason cultivars (with weak photoperiodic control), irrigation should be withheld until shortly before the desired floral initiation period (96).

The effect of irrigation after floral initiation has begun is less ambiguous than the results of pre-initiation watering. The number of fruit and fruit yield can be substantially increased by irrigating during initiation (146, 147, 181, 207). For established plantings this period is considered one of the two crucial times for irrigation (68).

In the spring there are two distinct responses to soil moisture during the course of reproductive development. The maximum number of flowers and fruit results from a period of irrigation prior to full bloom (146). This can greatly influence yield, since it is closely related to fruit number. Irrigation from full bloom until mid harvest increases fruit size (40, 94, 112, 146). But irrigation starting at the peak of the harvest, which typically lasts three weeks, did not improve fruit size or yield (146).

Strawberry growth response to irrigation may also depend on the method of irrigation. Drip irrigation, with frequent applications, may promote leaf expansive growth and improve survival or vigor of young plants. It can optimize growth with one-third the water of sprinkler irrigation and one-sixth of the requirement of furrow irrigation on sandy soil (123). Drip irrigation has not been shown to directly improve strawberry fruit yield over yields obtained with other systems of irrigation (113, 145). However, it can increase yield indirectly, as a means of applying fertilizer to sandy soil in several small increments (123), or by allowing an increased plant density compared to furrow-irrigated single rows (205).

Response to Nutrients

Nutrient requirements are not extremely high for strawberries, hence on reasonably fertile loam soils no fertilizer response can be detected (79, 148). Strawberries on sandy soil respond to nitrogen, phosphorus, potassium, and some micronutrients (123). Heavy nitrogen fertilization in late summer can delay floral initiation for up to 12 days, an effect parallel to that of August irrigation mentioned previously (12, 147).

Response to Polyethylene Mulch

Strawberries derive their name from the traditional practice of growing them with the aid of straw mulch. In the last 20 years polyethylene film has been used, and several colors have been tested under widely varying conditions. Vegetative growth is often increased but yield response has varied greatly, even at a single site during different years. In Italy black polyethylene increased fruit yield 8% in a dry year with no irrigation compared to 69% with irrigation and no mulch (49). In California clear polyethylene considerably increased the valuable early yield of fruit, but had little effect on total yield (46). In England both black and clear mulch increased fruit production, with the clear polyethylene superior in a cool summer and the black mulch better in a warm summer (9). The two largest effects of mulch are probably to increase soil and leaf temperature and to prevent surface evaporation of soil moisture. Clear polyethylene increases soil temperature more effectively (9), and both clear and black mulch probably increase leaf temperature. Another effect of mulch, which has not been evaluated, is the noticeable improvement in structure of a loam soil when it is protected from exposure to rainsplash and wind. The friable surface layer may be conducive to increased root development in the upper three inches, where the maximum potential for nutrient uptake may exist. On sandy soils mulching may prevent nutrient leaching during heavy rainfall (128).

Response to Plant Population

Plant population and arrangement of strawberries have been frequently studied, but results in terms of maximizing fruit yield have been variable (8, 38, 40, 130, 164, 168, 207). In general, it appears that cultural requirements such as equipment and picker access limit the population to suboptimal levels, usually only 20,000 to 25,000 mother plants per hectare. Thinning runner plants during the mat forming season increased yield compared to unthinned matted rows (207) or unthinned solid beds (164), where plant populations ranged from 250,000 to 900,000 plants per hectare. However, a solid bed which was thinned in late winter did not yield as well as its unthinned counterpart, even though plant population ranged from 1.2 to 1.6 million plants per hectare (8). When high density plantings were used to increase the first year yield, removing 50% of the plants improved the second year yield (38). A cultivar like 'Olympus' which is the subject of the current study, has a low tendency to produce stolons, and responded very favorably to placement into a closely spaced double row with 65,200 mother plants per hectare (131).

Response to Post-harvest Defoliation

The question of whether fruit yield can be increased by defoliation following the preceding crop was much stuied in the 1960's. It has been found that mature leaves can inhibit floral initiation, but the inhibition is reduced at shorter photoperiods. Young leaves reduce the effect of mature leaves, presumably by acting as sinks for the hypothesized hormone, which promotes vegetative growth and inhibits floral initiation (194). This led to work in Scotland which found that in some years removal of leaves resulted in a severalfold gain in yield (83). The causal relationship between increased inflorescence initiation and increased yield was demonstrated by 1966 (84), along with a basis for the observed cultivar differences (132). These differences concerned photoperiodic control of initiation, which was discussed previously. Environment may interact with cultivar, such that early cultivars grown at high latitude are most disposed to the problem of crown barrenness (i.e., the failure of inflorescence development). This was apparently the basis for an increased fruit yield following defoliation in Scotland, where crown barrenness is greatly reduced by this practice. When the same cultivars and procedures were used in England no benefit of defoliation was seen (95). And for three cultivars in the United States a lack of yield response to defoliation was also noted (140). Post-harvest defoliation is widely practiced, but the only definite advantages are cultural convenience and disease or pest control. However, the responses to irrigation, along with the observations in Scotland (84), suggest that strawberry growth responses to the whole range of cultural practices used will only be clearly understood when the control mechanism of floral initiation has been elucidated.

Water Relations Physiology

Plant Water Status and Response to Water Deficit: General Overview

Plant water status has been evaluated by several means, the most favored in recent years being the thermodynamic approach. This centers on the concept of water potential (ψ), the chemical potential of the water at a given point in the soil-plant-atmosphere continuum relative to an assigned $\psi = 0$ for pure water. The major components of ψ are the hydrostatic pressure potential (ψ_p), the solute potential (ψ_s), and the matric potential (ψ_m). Minor components are considered in more extensive analyses (210, 223). An alternative to the water potential component model was proposed by Spanner (186). The matric component is usually considered to be minor in tissue hydrated to more than 60% of full turgidity (210). As a result, the working equation frequently used is: $\psi = \psi_p + \psi_s$. The other widely used measure of water status is the relative water content (RWC), the tissue water content relative to full turgidity, expressed as a percent. Current procedures for RWC determination (184) are refinements of the method of Weatherly (17). A unique relationship between RWC and ψ has been described (74), but the assumptions required are not always valid, since the components of ψ may change in adjustment to water stress (4, 71, 199).

Attempts to characterize the flow of water through plants constitute a major area of water relations research. The driving force for water movement is a gradient in ψ, with flow from regions of higher to lower (more negative) ψ. A widely used analytical model equates fluxes of water vapor with the ratio of a driving force to a collective resistance term, as in Ohm's Law. Most water movement through plants is due to transpiration, in response to the relatively low ψ of atmospheric water vapor. Studies which have focused on determinations of resistance (R) to flow within plants, to explain, for instance, the variable response to drought by different species, have led to surprising conclusions. When transpiration rates were increased by lowering the relative humidity the calculated resistance in some species dropped considerably, which was suggested to be a departure from Ohm's Law behavior (18, 188). The site of reduced resistance was presumed to be the root system. Boyer (31) has provided an alternative explanation, wherein the apparent decrease in R with greater evaporative demand is due to a greater proportion of flow occurring along the transpiration pathway, which bypasses the leaf protoplasts and has a lower resistance than is required for movement into tissues where growth is occurring (31, 34). Root resistance only becomes dominant when the high protoplast resistance is bypassed. The driving force for water flow, i.e. the depression in ψ in the upper plant compared to the soil water, is also determined by the plant's aerial environment (e.g., the above mentioned response to altered humidity). A large body of literature has characterized such environmental effects on plant ψ (13, 24, 138, 185). As the soil dries out and its ψ drops, the leaf ψ may become independent of the atmospheric conditions, either due to increased flow resistance in the soil or plant regulation of transpiration by stomatal closure (19).

Another major area of water relations work is the determination of the relative sensitivity to water stress of different physiological processes such as leaf expansion, cell wall and protein synthesis, stomatal regulation, photosynthesis, and translocation. Several good review articles have summarized the data (21, 32, 92, 93). Hsiao (92) has ranked the processes in the above tentative order of decreasing sensitivity. Stomatal closure reduces water loss more than photosynthesis, since water loss is a linear function of conductance, while photosynthesis has additional resistances and is therefore not as directly linked to stomatal conductance (160). Effects of water stress on leaf expansion and stomata will be treated in more detail below. Inhibition of photosynthesis by water stress was summarized by Boyer (33), and includes effects on the CO_2 flux due to stomatal closure, and effects at the photochemical and CO_2-fixing enzyme levels (5, 30, 151). The translocation pathway appears to function under fairly severe stress, although the flow of assimilates decreases in response to reduced photosynthesis or growth (143, 208).

Drought resistance mechanisms of plants have been studied for many years, but have yet to be well defined. Desiccation tolerance and avoidance are two commonly distinguished categories (99), although a single species may possess water-conserving avoidance mechanisms during vegetative growth and dehydration tolerance during seed formation (77, 21). Two major physiological adaptations in the desiccation avoidance category are stomatal closure and increased production of solutes (osmotic adjustment), both of which will be discussed in more detail below. Morphological adaptations have also been noted, such as a reduced shoot/root ratio (154). Considerable evidence has pointed to a time factor which must be considered when evaluating stress response. This not only involves the stage of plant development or leaf age (107, 182), but also the previous history of stress exposure (39, 56, 193) and the rate at which stress develops (105, 137). Drought tolerance or water use efficiency can also be reduced by nutrient excesses or deficiencies (21). Recent texts have compiled physiological and biochemical findings on drought resistance which point the way to an improved functional understanding of plant response mechanisms (144, 152). Boyer and McPherson have offered basic guidelines to improved plant drought resistance through breeding and management (32).

Turgor (Pressure Potential) and Cell Enlargement

While water movement is determined by gradients in ψ, it has become evident that physiological processes are more directly related to specific components of ψ, especially to ψ_p, the pressure potential. When a physiological model has been conceived and sufficient data collected, one of the approaches to quantifying growth is to construct a physical model which is manageable yet approximates the behavior of the biological system. The basic equation used to describe the rate of cell enlargement or growth (G) is:

$$G = E\ (\psi_p - \psi_{p\ TH})$$

where E is the extensibility and $\psi_{p\ TH}$ is the threshold turgor level required for any enlargement to occur (124). The conductivity of the cell to water is incorporated into this simplified equation by assuming it is much larger than the extensibility and that expansion is therefore extensibly controlled (161). This may not be valid in all higher plant systems, so a more detailed equation may be required (50). Factors like temperature, nutrient status, and hormone levels probably exert their effects on the extensibility term. The field of turgor and cell growth is a dynamic one since it interrelates the mechanical properties of cell walls, the mode of action of hormones, and ion transport properties of membranes. The modulus of elasticity of the cell wall (ε) is a major component of E, the cell extensibility, and has been widely studied as a factor which may be altered in response to water stress (45, 58, 59). Altered eleasticity is inferred when the change in RWC is not constant with a given change in ψ_p, since $\varepsilon = \Delta\psi_p \div \Delta RWC$. An increase in elasticity could maintain cell turgor during desiccation (65), however stress preconditioning has actually been found to halve elasticity in sorghum (104). Analysis of the growth equation in terms of auxin effects suggests that auxin could convert a non-enlarging cell into an enlarging one in 3 or 4 possible ways, however the only observed means is by an increase in extensibility (50). This mechanism probably involves H^+ ion extrusion through the membrane and a biochemical loosening of bonds in the cell wall polysaccharides (162, 50). Another body of literature suggests that the maintenance of adequate ψ_p for expansion is part of a self regulating process, where ψ_p acts on the membrane conformation to control active ion transport (87, 226). However a study using onion epidermal cells led to a contrasting view (153). The cell growth-turgor relationships discussed above have been applied to leaf, stem, and root growth (50, 59, 78).

Osmotic adjustment, an increased solute level in response to water deficit, may be a specialized aspect of a basic metabolic process, the self regulation of cell osmolarity (53). The added solutes increase the ψ gradient for water movement into cells and therefore maintain ψ_p. In most crop plant systems studied to date, the bulk of the newly synthesized solute consists of soluble carbohydrates or organic acids rather than salt ions(4, 50, 65, 71, 199). Good reviews have been written by Hsiao (92), Hellebust (89), and Zimmermann (227), and include discussion of systems involving either K^+ ions or organic acids such as malate. The role of gibberellin in some systems will be discussed below. ψ_p maintenance by osmotic adjustment has been shown to allow growth of both leaves (92) and roots (137) at ψ values which prevent growth when plants are rapidly stressed. Reductions in photosynthesis may also be avoided since it is usually less sensitive to desiccation than leaf growth is (92). The increased solute in soybean hypocotyls was derived by hydrolysis of seed carbohydrate (137), while expanding leaf cells take up sucrose derived from photosynthesis and increase the solute level by invertase activity, a process which apparently tolerates low ψ (89). Additional mechanisms of soluble carbohydrate and organic acid accumulation probably exist. These may be the basis for the "time factor" for stress adaptation discussed previously. A related form of adjustment to stress was proposed by Cutler (57) in which reduced cell size allows better ψ_p maintenance due to a higher proportion of tissue water being held in the cell wall. The lower volume of symplast water has a lower ψ_s due to the greater solute concentration.

The direct measurement of cell turgor is a major current goal of water relations methodology. Pressure probes are in use with large algal cells (226), and microcapillaries have been used on single guard cells (135), although the absolute values derived by the latter method are held to be questionable by Zimmermann (227). The standard methodology involves an indirect calculation of ψ_p, using the equation $\psi = \psi_p + \psi_s$. The total ψ is measured by psychrometry (27) or is estimated from the xylem pressure potential, measured with a pressure chamber (165, 209). Determination of ψ_s is commonly made using sap expressed from frozen tissue in a psychrometer or dewpoint hygrometer (44), but may also be derived by the pressure-volume method in a pressure chamber (48, 219). ψ_p is then calculated by difference, assuming that other components including ψ_m are negligible. An alternative psychrometric method (30) produces a value which includes both ψ_s and ψ_m. A frequent result when using the pressure chamber for ψ estimation and a ψ_s value from frozen sap in a psychrometer is that negative ψ_s values are produced. This has been defended as biologically possible (150, 210), however Boyer and Potter (30) and Tyree (201) have pointed out the dilution effect of apoplastic water on the cell sap following tissue freezing, which increased the ψ_s reading. This caused ψ_p to be underestimated by 7% for sorghum tissue at 100% RWC (199) and the error may increase as RWC declines (222). Shepherd (176, 177) considered another possible source of ψ_p underestimation, the assumption that $\psi_m = 0$ in expressed sap, and concluded that ψ_m could only be ignored if the range of ψ_p rather than ψ_s was known to be several times that of ψ_m. His data on wheat offers a rare exception to the rule that ψ_m is negligible in mesophytes at physiological levels of tissue RWC (28). Barring more data like that of Shepherd, it is probably safe to calculate ψ_p as ψ minus ψ_s, and then adjust for the dilution effect as Boyer did (30), if so desired.

Leaf Expansion

Cell pressure potential (ψ_p) is probably the only driving force for cell and leaf expansion, because expansion has never been observed at zero turgor. As Cram (53) points out, this does not mean that it determines the rate of expansion, except in the lower range of ψ_p. Limitations in growth can, of course, be imposed by a range of factors, including low temperature (4), inadequate daylength (12), or nutrient deficiency. Even a small drop in ψ_p rapidly reduces the short term rate of leaf elongation (221), although partial or full recovery usually occurs without restoring the original ψ_p level. Medium term leaf expansion (over hours or days) has been widely shown to decrease or stop with relatively mild stress (29, 51, 73, 92, 101, 102). Long term measurements also showed that final leaf area was correlated with the mean leaf ψ (110, 183). It was not clear whether the effect on cell enlargement was the sole factor, of if cell division and rate of leaf initiation were also involved. In tobacco leaves cell expansion and leaf initiation were both much more sensitive than cell division (51). In sorghum cell division was held to be as sensitive as the cell expansion rate (133), however, the conclusion was based on epidermal cell counts, which may not provide a valid estimate. In sugar beet leaves cell division was greatly reduced by a mild stress without reducing the mean cell volume (192). Cell division of radish cotyledons was reduced more than cell length at a turgor of 5 bars compared to 6 bars (111). It appears the question of relative sensitivity to reduced ψ_p is far from settled, and the answer may vary for different species and ontogenetic stages.

Frequent studies have been made on the rates of leaf expansion during diurnal cycles for greenhouse and field grown plants. Both linear (41) and curvilinear (16) relationships between leaf expansion and ψ_p have been observed. A linear increase in expansion up to the maximum turgor levels seems unlikely, but it cannot be ruled out. In other cases low temperature limited growth at night so a multiple regression relation on ψ_p and temperature better characterized elongation (3). In yet other cases leaf elongation (averaged over more than an hour) continued at a constant rate despite a midday drop in ψ_p, resulting in apparent modulation of leaf elongation by temperature and radiation only (221). "Stored" growth may be common, in which factors for wall extension accumulate despite a transient loss of cell expansion due to low ψ_p. Rapid growth resumes when ψ_p is restored, assuming temperature is favorable. Variable species response may be due to the ability of some crops to osmotically adjust. Well irrigated sugar beets had a maximum leaf elongation rate at sunset, and showed a shart decline between sunrise and 8 AM, with little midday growth (102). At the same location sorghum, now known to osmotically adjust during the daytime drop in ψ (4), had a peak leaf elongation rate midday, and reached a minimum in early evening (101). However, it appears that on a seasonal basis leaf growth is reduced by drought despite apparently equal midday ψ_p (82). This may be a direct effect of low ψ_s, or of high salt levels (in those species which lower their ψ_s levels with salt ions). An additional important aspect of leaf growth is the characterization of how it interacts with other metabolic factors to determine total plant growth. The degree of partitioning of photosynthate into additional leaf area appears to be an important determinant of the relative growth rate (157). For soybeans and cotton at a range of humidity environments, low ψ_p did not always reduce leaf expansion and dry weight gain was only reduced when leaf expansion was. However, the relative importance of leaf expansion and net assimulation rate depended on the degree and duration of stress (42). A good attempt to integrate current knowledge into a dynamic model of crop growth and yield responses to water stress was presented by Hsiao et al. (93).

The methodologies for leaf expansion measurements are straightforward. Leaf area is most conveniently measured on detached or intact leaves with electronic area meters. Leaf or leaflet area growth is often proportional to 2-dimentional elongation during intervals of a few days or less, and in many species length changes can be measured with a ruler after 2-6 hours. Short term, nearly instantaneous elongation can be monitored with a linear variable differential transducer (LVDT), or variation thereof (91).

Strawberry leaf growth does not appear to involve any exceptional factors that would complicate its study. It is quite sensitive to the daylength, with greater final size attained during longer days (12). In that study it was concluded, based on counts of epidermal cells, that daylength produced its effect via early cell division, and the final leaf size was a function of cell number. Later work, (1) using cell macerates, showed that the daylength effect actually occurred in the later stages of leaf expansion. After leaf emergence the enlargement process involves both cell division and expansion, but final leaf size is controlled by the duration of cell expansion, which varies during the season (1). Comparisons of elongation of stressed and unstressed leaves have not been made.

Stomatal Behavior

Stomatal behavior is a key aspect of leaf water relations, and it has been the major research focus during the 100 years that the regulatory role of stomata has been suspected. Raschke (160) reveiwed the plant's dilemma of opposing priorities, namely, the need for intensive gas exchange between the mesophyll and atmosphere to supply CO_2, while keeping exchange low in terms of water loss. The stomatal role in drought resistance is of the desiccation avoidance type. Transpiration may be restricted when soil moisture is low or when evaporative demand is high. To assess the degree of stomatal control of plant water status, a method such as that of Jones (103) can be used.

The search to elucidate a control system for stomatal function has identified light, water status, nutrient status, temperature, humidity, hormone levels, and the concentrations of CO_2 and some gaseous pollutants as factors that effect stomatal aperture (196). Interactions among the factors are also reasonable to expect (100, 214). Light level and water status are probably the major factors in field crops. Species variation is considerable in terms of the irradiance required for complete stomatal opening and the critical range of ψ or ψ_p at which stomata close to reduce transpiration (196). Despite the wide array of reports that stomata show a switch-like response to a critical ψ value, one explanation for this behavior is that it is due to rapidly induced stress and non-adapted plant material (155). Another expanation is considered below. When stress develops slowly the range of ψ for closure may be greater than 10 bars (105). It is also likely that a universal mechanism of stomatal movement does not exist. Work on a variety of plant systems has generated several proposed modes. Guard cell turgor (ψ_p) is the immediate determinant of aperture (72). Increased ψ_p for opening may be induced by guard cell uptake of K^+ ions, in exhange for H^+ ions. This is accompanied by a production of organic anions from carbohydrate reserves, or by the import of Cl^- ions, depending on the species (160, 174). The effect of light in the morning may be to deplete internal leaf CO_2 and trigger the H^+/K^+ exchange (160). The effect of water deficit was initially felt to be a reduction in guard cell turgor in response to declining bulk leaf ψ_p. However, stomatal conductance is reportedly unaffected in many species over much of the range from maximum ψ_p to values below 3 bars, so that the guard cell-subsidiary cell balance may be independent of bulk ψ_p (198). However, the range of ψ_p for stomatal closure in different species is much narrower than the range of ψ values. This is expected since changes in total ψ are only likely to correspond to changes in physiological processes when there are no alterations in ψ component relationships, such as osmotic adjustment (92).

In the past 10 years considerable data on stomatal function has documented the involvement of hormones, and the mechanisms of these responses are currently being integrated with the other control factors. A general discussion of hormones and water relations physiology will follow; only abscisic acid (ABA) is considered here. Wright and Hiron (224) reported an increase in ABA in wilting detached leaves and then in wilting or flood-stressed intact plants (90). Exogenous ABA in the transpiration stream causes stomatal closure, and the response is rapidly reversible (55). ABA induced closure requires CO_2, and in Xanthium it acts by sensitizing the stomata to CO_2 (159). Pre-chilling also increases CO_2 sensitivity (70). This is known as hydroactive closure since guard cells lose K^+ ions, perhaps due to an ABA blockage of H^+ extrusion (160). Several papers reported rapid increases in leaf ABA levels and stomatal closure over a narrow range of ψ in water stressed plants (7, 20, 120, 225). A recently refined hypothesis of ABA action by Mansfield et al. (129) states that ABA is contained in chloroplasts of mesophyll (and not guard) cells and is released and also synthesized in response to water stress. The ABA moves through the symplast to subsidiary cells, then crosses to guard cells where it remains active even after leaf ABA levels have dropped in response to turgor restoration. ABA-induced closure may occur gradually as leaf ψ declines, rather than at a threshold ψ. The threshold concept was derived from plots of stomatal resistance vs. ψ, which are often quadratic in nature, with a sharp inflection point at which resistance rapidly rises. The choice of resistance, rather than its reciprocal, conductance, may have unforseen consequences. The mathematical nature of reciprocal transformation includes the possibility of converting a linear function into a quadratic one. If the inflection point is to be given physiological significance then there must also be a physiological basis for choosing the quadratic function, otherwise one is dealing with a mathematical artifact. When conductance and resistance are considered in relation to transpiration, the usual finding is that transpiration is a linear function of conductance (198) and cannot, therefore, be as simply related to resistance. Since the rapid increase in resistance does not correspond to an equally rapid decrease in transpiration the ψ value at which the inflection point occurs should not be considered a threshold value for stomatal closure. The concept of an on-off switch, while appealing, derived from resistance data, which was by its nature data that was transformed before it was examined.

The ABA mechanism is considered the "second line of defense" against desiccation, since transpiration in many species is also regulated by direct stomatal response to the aerial environment, such as the vapor pressure deficit and CO_2 concentration (129). This is the basis for the many reports of response by stomata to lowered humidity (43, 69, 116, 138) as well as the response to wind (43, 61, 66, 69). Another humidity response which could change the total leaf conductance is the alteration of cuticular resistance (141). The wide range of responses included in the two stomatal "lines of defense," combined with the variety of combinations of these adopted by different species, is probably the basis for much of the past confusion and the slow progress in unravelling the complexities of stomatal behavior.

An area related to the direct sensitivity of stomata to humidity is the determination of transpiration pathways in leaves. The standard conception is that water flows from vessels through mesophyll cell walls and evaporates at mesophyll cell walls lining the substomatal cavities. This view can be challenged due to increasing amounts of data which show the greater efficiency of water transport along epidermal cell walls than in mesophyll cell walls (178). A close hydraulic connection of epidermis and vascular tissue was indicated for a mesophytic species, while this was lacking for a xerophyte (178). A species like sunflower apparently does not greatly restrict transiration flow even with a high evaporative demand, so that photosynthesis will be maintained at a high rate. This requires very efficient water transport (86). Boyer (34) has suggested that high resistances are avoided in sunflower by evaporation of water close to the xylem with subsequent flux in the gas phase. The pathway of water movement into cells to drive expansion would therefore be separate, with the vapor path controlling leaf ψ when transpiration was rapid and the protoplast path controlling leaf ψ in the range where growth is possible (34). This offers a mechanism of control of leaf growth which integrates the evaporative demand without directly involving the stomata. Work by Meidner et al. (135, 136) suggested that considerable water flow occurs from veins through epidermal tissue and evaporates near stomata. This evaporation provides a rationale for the large solute buildup in guard cells, since the low ψ_s is required to compete with the evaporative pull for the available water. A more controversial interpretation of similar data is that the major hydroactive control of stomata is by peristomatal transpiration from both internal and external surfaces of guard and subsidiary cells (126). Supply and demand variables are integrated by competition between the guard cell, the atmosphere, and the subsidiary cell for water in the epidermis. This work, along with that of Meidner (136) and Boyer (34) offers an explanation of how guard cell turgor may reflect evaporative demand directly rather than through bulk leaf ψ or ψ_p.

Stomatal behavior is also affected by a range of secondary factors which must be considered if comparisons of data are to be valid. Nutrient status must be known, since both N and K deficiencies reduced stomatal aperture of well watered plants, but stomata did not close as tightly in dry soil conditions when N was deficient (179, 21). The degree of osmotic adjustment is also reduced when N is low (180). Leaf age must also be uniform, since stomatal conductance (K_{st}) usually increases until the leaf approaches full expansion and later declines (107). The elastic modulus and components of ψ differ with leaf age (220). The relation of K_{st} to ψ also changes for plants at different growth states (182). In some species K_{st} is very sensitive to low irradiance, so that the relation of K_{st} to ψ may vary for leaves at different heights in the canopy (198).

Stomatal behavior has been studied using a wide range of methods. A fairly comprehensive bulletin on methodology is available from 14 western states, which cooperated in conducting the research (e.g., 211). Direct microscopic observation of aperture is still useful in some cases.

Leaf impressions made with quick setting materials are frequently more convenient and precise (172). Stomatal conductance or resistance has in recent years been calculated from measurements of water vapor flux out of leaves, using portable diffusion porometers (195). The theory, calibration, and use of such devices has generated much discussion (115, 134, 142). It is safe to conclude that proper use and a consistent calibration procedure will allow data that is reproducible and useful for relative comparisons among treatments. The calculated values of leaf conductance cannot be taken as absolute for most porometers (115).

A final problem is the determination of what range of leaf conductance or resistance is most physiologically significant. Usually a microscopic check is used to see what K_{st} value is indicative of stomatal closure. However, Shimshi (179) has suggested that much of the reduction in transpiration occurs with continued closure after passing the point of visual resolution.

Stomatal behavior of strawberry leaves has received very little study. Visual techniques in the 1930's detected stomatal closure in response to the daily increase in evaporative demand, which occurred much earlier and more extensively with low soil moisture. Stomata were more open in a humid greenhouse (61). A recent study of photosynthesis during flowering showed a rapid decline as leaf ψ dropped from -3 to -6 bars (118). At this ψ level photochemical effects are unlikely, so that stomata may be inferred to be quite sensitive to desiccation at the flowering stage.

Hormonal Control of Water Relations

Elucidation of hormonal water relations control mechanisms in plants is in the very early stages, although some notable effects have been detected, as reviewed by Vaadia (202). Abscisic acid, in addition to its role in stomatal regulations, has been found to increase the permeability of cells to water (76). This may be important in the roots, where decreased resistance to flow would be a desirable response to water deficit. Root resistance is in fact decreased, as is stomatal conductance, when ABA is supplied to wilty tomato mutants, which have high cytokinin levels and low natural ABA levels (190). Potassium ion transport by roots is inhibited by cytokinin (202) and stimulated by ABA under some conditions (156). Exogenous ABA can also alter the leaf morphology of wheat in a fashion very similar to prolonged water stress, which suggests it is the mediator of such adaptive responses (158).

The overall system of hormonal control is probably based on the balance of growth regulators rather than the absolute concentrations of each. The root exudates of water stressed plants have reduced levels of cytokinins (97). Kinetin increases stomatal aperture and transpiration (121), and therefore works in the opposite direction of ABA. Kinetin restores transpiration of stressed plants to the level of non-stressed plants, while ABA reduces transpiration of non-stressed plants to the same degree that water stress does (139). Gibberellic acid (GA) also increased transpiration in barley (121). The implications are that the mechanisms of transpiration control may involve shifts in the endogenous levels of these hormones. The role of auxin in the elongation of cells and stems or coleoptile sections has been discussed previously. Cleland (50) concluded that in intact pea stems auxin supply is adequate and is not a distinguishing factor between dwarf and tall peas. He pointed to the tugor pressure rather than the cell wall loosening of auxin as the seat of elongation control. Hormones re-enter the picture, however, since tugor in pea stems is apparently a function of osmotic adjustment and GA regulates the enzymes which produce the osmoticum (50).. Ethylene has been found to increase along with ABA in stressed leaves, so it may have a role also (35). The involved methods of hormone analysis have contributed to the relatively slow beginnings of that research area. Expensive and time-consuming laboratory procedures are required to extract and measure endogenous levels.

Growth Environment Effects

Since much of the data on water relations physiology has been derived from plants in controlled growth chamber or greenhouse environments which differ greatly from field conditions, it is important to consider the effects of environment on plant morphology and function. Leaf thickness is greater for field than chamber and greenhouse grown soybean and cotton plants, although low night temperature in the growth chamber may overcome this difference (204). Stomatal sensitivity to low light was much greater for soybean and cotton plants in the two indoor environments. Stomatal sensitivity of well-watered plants to decreasing midday leaf ψ was greatest in chamber-grown plants and least in field-grown plants (67). Decreased sensitivity of field plants is probably a result of "hardening" under frequent mild stress, by such means as osmotic adjustment. This is supported by studies of controlled stress-conditioning (39, 56, 193). A more rapid rate of stress development, as experienced by plants in small containers, was shown to result in no solute accumulation (for osmotic adjustment), and lower rates of photosynthesis and leaf conductance at any given leaf ψ. With a slow rate of stress development rapid stomatal closure at a threshold ψ failed to occur (105).

The differences existing between the field and controlled environments usually result in different types of drought stress, since above average radiation and temperature and low humidity often accompany restricted water supply in the field, while water supply may be the only variable in growth chambers. The "square wave" light and temperature regimes of growth chambers are possible factors, although the restricted root zone and more rapid drying of indoor plants is probably a more important factor (106). Potted plants grown outdoors showed the same responses to water stress as plants in a high irradiance growth chamber, and were more sensitive to stress than would be expected for plants in the field (125).

The same problem of growth environment and pre-conditioning arises when determining leaf elongation sensitivity to stress. High sensitivity to reduced ψ occurs in chamber grown plants (29), with growth ceasing at ψ values which are common throughout the day in the field. This led one research group to conclude that maize does not grow during the day (163), yet active growth has been measured by others (4, 213). The elongation characteristics of leaves in greenhouse and outdoor potted plants were duplicated on chamber plants by subjecting them to mild and moderate water stress, respectively, so that the average ψ of these environments was matched (41). Despite the lower ψ_p values for potted plants outdoors, the 72 hour leaf elongation rates were all equal. As more field data accumulated, showing that leaf growth was relatively insensitive to ψ_p fluctuations, it became reasonable to question the principle that wide differences exist in the sensitivity of different plant processes to water stress. Wenkert et al. (221) found that short term sensitivity of leaf elongation to reduced ψ_p was compensated for over longer periods. They suggested that the real limitations to growth, within the range of adaptation, are general metabolic ones including photosynthesis, sink competition, wall loosening, membrane permeability and solute production along with cell turgor. Many of these are subject to temperature or hormonal modulation. Another possible modulator of metabolism during water deficit is ATP, since ATP levels in the elongation zone of corn leaves decreased 40% within 3 hours of stress induction (15). Whether or not the interactions and compensating responses among the various aspects of metabolism prove inseparable remains to be seen. It seems possible, based on species comparisons, that the effects of turgor driven leaf expansion will prove to be the primary determinant of growth. Much remains to be explained regarding the large reductions in final leaf area despite maintenance of ψ_p and leaf elongation rates during the intervals examined (4, 39, 221). While ψ_p may not be the all-controlling factor, leaf expansion potential may still prove highly sensitive to water stress compared to other plant responses.

The processes of water relations physiology display a fluidity which makes them very challenging to characterize. They bring to mind the statement of Webb (218) that biological systems are gestalten. Factors which are defined by being isolated in time or space must eventually be understood as they exist in dynamic whole systems. How do we proceed, then, from the point of current understanding? It is apparent that the literature information to date is either tentative or hypothetical. It will probably be necessary to continue on these two tracks in the immediate future, using refined methods and measuring devices to accumulate data which is less tentative and which can be used to test and alter hypotheses. The crop-oriented disciplines can make important contributions of this nature. For an aspect of plant function such as stomatal behavior, which may not have a single mechanism in all plants, the most successful approach to determining the underlying principles may be inductive, using data from groups of crop plants which behave similarly. Such data may serve a dual purpose if it also characterizes a crop response which is useful as an index of how cultural practices and environment effect the crop. For instance, if the leaf elongation rate (LER) of strawberries proves to be a sensitive measure of water stress and the differences in LER are reflected in fruit yields, it may be possible to better optimize irrigation scheduling. Fruit yield is subject to modification by more variables than is leaf elongation and is therefore a more difficult criterion for irrigation testing of cultivars. Such data may therefore find immediate use as a guide to cultural practices and breeding efforts, and also be useful in the long term elucidation of water relations physiology.

VEGETATIVE GROWTH RESPONSE OF 'OLYMPUS' STRAWBERRY TO POLYETHYLENE MULCH AND DRIP IRRIGATION REGIMES

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Additional index words. leaf area, number of crowns, Fragaria x ananassa

Abstract. Two field plantings of Fragaria x Ananassa Duch. cv. Olympus strawberries were grown with and without black polyethylene mulch at 3 rates of drip irrigation (0, 0.23 and 0.70 of pan evaporation). After plant establishment differential irrigation was maintained for 1 month in 1977 and 2 months in 1978. During the driest portion of each year the soil water potential at 20 cm depth remained above -0.3 bars for the highest rate of irrigation with mulch, and fell below -11 bars at the lowest rate without mulch. Vegetative growth was in all cases significantly increased by both irrigation and mulch. The number of leaves produced during the first season of the 2 plantings was 25 to 30% greater in the mulched than the unmulched treatments. The gains in the number of crowns were similar. The number of leaves which were present early in the following summer was significantly higher for mulched treatments, and leaf area showed an even greater increase. During a second year of treatments on the 1977 planting the number of leaves was increased 75% by irrigation (highest vs. lowest), and 39% by mulch while crowns made lesser gains. In spite of the much greater number of leaves at fruit harvest on 2 year vs. 1 year old plants, the total plant leaf area averaged 27% lower. Leaf and crown dry weights just after fruit harvest were slightly greater due to irrigation and

significantly higher due to mulch, while root dry weight was unaffected by either. The amount of irrigation required to sustain vigorous vegetative growth when mulch is present is less than half of the recommended rate for sprinkler irrigation without mulch.

Introduction

A 1967 review concluded that strawberry growth and fruit yield can often be increased by supplemental irrigation (13). Regular irrigation is recommended throughout the first season in regions with dry summers (4, 5). This has been found to maximize leaf growth and the formation of stolons (runners) (2, 6, 8, 12, 15).

Mulching and drip irrigation are two practices which provide refinements in strawberry irrigation. Frequent watering, which is more feasible with drip irrigation, allows maximum survival and leaf development of runner plants (12). Polyethylene film is the mulch material most commercially feasible, and clear poly has been in common use in California for 2 decades. In England plant size was increased with either clear or black polyethylene mulch (1).

In an earlier study, 'Olympus' strawberries were grown in single or double rows in raised beds with drip irrigation and black polyethylene mulch. The double rows produced 53 MT/ha, 5 times the average yield for Oregon (7). This cultivar produces few stolons and many branch crowns, an apparent advantage under these cultural practices. The current study focused on 2 components of this cultural system, drip irrigation and mulch, with the objective of evaluating the growth and fruit yield response to mulch and increased rates of irrigation. This paper will examine the vegetative growth response by 2 plantings (1977 and 1978), while flowering and fruiting responses will be considered in a subsequent paper (9).

Materials and Methods

Field plots of 'Olympus' were established on May 17, 1977, and again on May 11, 1978, using shaped soil beds 56 cm wide and 12 cm high. Porous drip irrigation tubing was used as well as a mulch consisting of 0.10 mm black polyethylene. After trimming roots to 10 cm length, plants of 10-18 g were set 38 cm apart in 12 single rows, which is equivalent to 24,700 plant/ha at a conventional row spacing of 107 cm. Actual row spacing was 205 cm to prevent irrigation water from reaching adjacent rows. Soil beds were 14.6 m long in 1977 and 19.5 m long in 1978. The soil texture was a sandy loam.

The polyethylene (P) was removed from half the length of each row when plants were well established. Irrigation was then applied at 2 to 3 day intervals at rates of 0, 0.23 and 0.70 of the water evaporated from a Class A weather pan, and are referred to as low (L), medium (M) and high (H) regimes. By comparison, a previous study on sandy loam soil found that strawberry consumptive use was fully supplied by an irrigation rate of 0.56 of pan evaporation, assuming 75% efficiency for sprinkler irrigation (4). Efficiency of drip irrigation is higher than sprinkler systems.

A split plot design was used, with 6 treatment combinations (3 irrigation regimes with and without mulch), replicated 4 times. The design was required due to physical restrictions on randomization caused by the use of drip irrigation and poly mulch. As a result the effect of mulch and the overall effect of increased irrigation could be tested by analysis of variance, but a 6-treatment comparison of all combinations of the 2 factors was not legitimate.

At each irrigation the flow rate was adjusted so that it was equal in the 4 replicate lines. The duration of each irrigation was calculated using an effective wetted width, which was itself determined by measuring lateral soil water movement with 2 lines of closely-spaced tensiometers placed across 2 soil beds of each irrigation rate. The width was in most cases 61 cm. During periods of rainfall clear polyethylene was supported above plants in the L and M regimes of the 1978 planting. Soil moisture was monitored 5 days a week at 54 sites in the 1977 planting, using tensiometers and gypsum blocks at 20, 60 and 90 cm depths. Soil temperature during the summer was continuously recorded in mulched and unmulched beds.

Neither planting was fertilized during the first year since previous work at this site found it to be unnecessary. For subsequent crops the standard time for fertilization in the Pacific Northwest is nearly a year prior to fruit harvest, when the resumption of active vegetative growth is desired. The 1977 planting, following the first harvest, was therefore supplied with soluble 30-4-8 NPK fertilizer through the drip system at the rate of 35.6 kg N/ha. The same irrigation treatments were then resumed for a second season.

The number of crowns, leaves and stolons were counted on 20 plants per treatment every 2-4 weeks until October of the first growing season. Stolons were removed at each counting. Plant size (height and width) was measured late in each growing season. During the second season of the 1977 planting, leaves and crowns were counted at the start of irrigation treatments (July) and again in September.

In 1979, following the first fruit harvest from the 1978 planting and the second harvest from the 1977 planting, 5 plants per treatment were carefully dug and the roots washed free of soil. Crowns and inflorescences were counted and the area of a subsample ($\sim$30% of the total) of leaves was measured with an electronic area meter. Total leaf area was calculated from the specific leaf weight of the subsample and the total leaf dry weight. Leaf, crown, and root dry weights were determined following 48 hrs at 65° C.

Results and Discussion

Growth environments. The patterns of evaporative demand during the summers of 1977 and 1978 were similar (Fig. 1). In 1977 differential irrigation was maintained during 13 applications until heavy rainfall occurred (Table 1). Minimum soil water potential (ψ) ranged from -0.1 bar for the H and HP treatments to -11.6 bars for the L treatment (Fig. 2A). Rainfall kept soil ψ values quite high for all treatments after August 26, so that only one additional irrigation was required on September 12 for the M and H regimes. Soil temperature at 7.5 cm depth averaged 4°C warmer under mulch following a typical hot day, with the greatest difference during the night and the least difference midday. Temperature elevation due to mulch was less than 1.5°C at 20 cm depth, and 2.5-3.0°C at 10 cm depth in 1978. See Appendix A for detailed soil temperature data.

For the 1978 planting the treatment period was longer, but only due to the use of rain shelters. A total of 22 irrigations were used (Table 1). The 1977 planting remained unsheltered in 1978, but the amount of water received differed from the 1978 planting only for L and LP treatments, which received 9.8 cm of rain. The minimum 20 cm soil ψ of the L treatment in the driest period was the same as in 1977 (Fig. 2B). The soil of the L, LP, M and MP treatments in 1978 dried more quickly than in 1977 and did not fully re-wet during the first period of rainfall (August 11), since much of it was diverted by the shelters. The minimum ψ value for MP (-.85 bars) was surprising, and may have been inaccurate due to the belated placement of the gypsum blocks. The next heavy rainfall started September 8 and raised the soil ψ to near zero for the M and MP treatments, which were uncovered. although the L treatment was sheltered, the soil was also re-wet, apparently by water moving laterally through saturated soil. This did not occur for the LP treatment due to the poly mulch on the sides of the beds, so soil ψ remained low for the following month. The H irrigation regime received 2 final irrigations on September 13 and October 14.

Growth responses. Irrigation and mulch both significantly increased vegetative growth, as monitored by counts of leaves and crowns (Fig. 3). Complete data taken during the year of planting is shown in Appendix B, Figures B-1 to B-4. In the 2 plantings there were 25 to 30% more leaves produced during the first season by the high (H and HP) than the low (L and LP) treatments. These results cannot be compared to past reports since the only other irrigation studies where extensive leaf and crown counts were made focused on newly-formed runner plants, which had an order of magnitude fewer leaves than the plants in this study (12). The mulched treatments totaled 27 and 14% more leaves than the unmulched in the 1977 and 1978 plantings, respectively. The gains in the number of crowns from both irrigation and mulch were of similar magnitude (Fig. 3B). The analysis of variance detected no significant interaction of irrigation and mulch on any parameters of vegetative growth, although in 1977 increasing irrigation tended to increase leaf numbers more when mulch was absent. Similarly, the positive effect of mulch on vegetative growth was greatest at the low rate of irrigation. This response pattern did not occur for the 1978 planting. Growth of the unmulched L and M treatments was less restricted in the 1978 than the 1977 environment, while the LP treatment had reduced growth in 1978, perhaps due to the lower soil ψ.

Mulch also had positive effects on vegetative growth during the second spring of the 1977 planting, since the numbers of leaves and especially crowns were greater on mulched plants right after fruit harvest in July, prior to the continuation of differential irrigation (Table 2). The plant size was 30% greater on mulched plants. This is similar to results in England (1) where black poly increased the size of plants at the time of the first crop (June or July) an average of 24% for several cultivars in 3 different years. The planting dates were in September rather than May, so the results cannot be fully equated. Plant size was a close function of the number of leaves and crowns (Table 3), and may therefore be a more convenient measure of vegetative growth for use in future work. After the second summer of irrigation the number of leaves and crowns, and plant size were again increased in response to both irrigation and mulch. The magnitude of the gains due to treatments was similar to the first season response in the case of crowns, but the percentage increase in number of leaves was much greater during the second season (July to September), with a 75% gain due to irrigation and a 39% increase from mulch (Table 2).

Enhancement of leaf area by mulch for plants of any age was greater than the effect on leaf numbers, based on visual estimates during the first season of each planting and leaf area measurements at the time of fruit harvest (Table 4). This is supported by measurements of the length of leaf laminae from the time of unfolding until full expansion, which showed that mulch increased final leaf size, even on plants at the H rate of irrigation (11). Also see Appendix C. Irrigation (H vs. L) also increased final leaf size in the summer (10), but the effect did not carry over to the following spring (see leaf area, Table 4).

Stolon production was proportional to plant size, except that in 1977 the plants from treatment HP were larger but had fewer stolons than those of H. The range of stolons/plant in 1977 was 3.3 (L) to 12.1 (H), and in 1978 was 12.9 (L) to 21.5 (HP). See Appendix Table B-1, for the complete data. Very few runners were produced in the second year of the 1977 planting. The increased stolon production with greater irrigation agrees with past counts of rooted runner plants (14, 15), but differs from another study (3). While the HP treatment had the most runners in 1978, it had fewer stolons than the MP treatment in 1977. Reduced runnering at high irrigation was also observed on mulched plants in California (3).

The data from the plants dug at the end of the trial are shown in Tables 4 and 5. The 14 month old planting (1978) did not show a significant increase in leaf and crown dry weight due to summer irrigation, perhaps due to an inadequate sample size (Table 4). Mulch treatments were in effect continuously, and the increase in leaf and crown dry weight was clear. The effect of mulch on leaf weight was likely a result of its dramatic enhancement of leaf area, since the two are closely related (see Table 3). In contrast to the effect on crown dry weight, the number of crowns was increased by irrigation but not by mulch. Neither mulch nor irrigation affected root dry weight or specific leaf weight. The large mulch effect on top growth without an increase in root weight resulted in significantly higher shoot/root ratios.

The same irrigation and mulch effects on the plant harvest parameters were found for the 2 year old plants of the 1977 planting, although with greater variability such that mulch did not increase crown weight significantly (Table 5). Specific leaf weight in this planting decreased with increasing irrigation (data not shown). Root dry weight was again fairly constant, but the roots and crowns had 45% and 30% higher dry weights, respectively, than those from the 1 year younger 1978 planting. In contrast, leaf area, leaf dry weight, and specific leaf weight were lower on the 2 year old plants. The shoot/root ratios were also lower. Average leaf area of 2 year old plants was 27% lower than for 1 year old plants at the time of fruiting, even though there were 92% more leaves on 2 year old plants.

Significant regression relationships were found between most variables where biological associations could be expected (Table 3). Simple linear regression proved equal to or better than multiple or quadratic relationships, except for plant size. It is also of note that leaf area in July, at the end of fruit harvest, was not significantly related to the number of current crowns (which includes new spring crowns), but was closely related to the number of crowns the previous autumn.

Conclusions

Although the irrigation treatment period was brief, the vegetative growth response was very positive. Black polyethylene mulch, which had a longer time to exert its influence, gave a generally greater growth response, especially in terms of size and dry weight of plant parts. The amount of irrigation required to sustain vigorous vegetative growth is probably not significantly lowered by using drip rather than sprinkler irrigation on loam soil. Since an irrigation factor of 0.23 times pan evaporation limits leaf growth compared to a factor of 0.70 when no mulch is present (Fig. 3A), the optimum factor for drip irrigation may be as large as the 0.56 value used for sprinklers (4). A direct comparison of drip to sprinkler irrigation is a prerequisite to making a general conclusion on the value of drip irrigation. Mulch probably enhances growth both due to the higher soil temperature and through soil moisture conservation. The LP treatment maintained good growth in 1977 with no irrigation during the month long treatment period, and near maximal growth occurred in both years in the MP treatment, which had half the irrigation rate used with sprinklers on this soil texture. Mulch therefore increased water use efficiency in terms of the vegetative growth of 'Olympus' strawberry.

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Table 1. Amount of irrigation plus rainfall (cm) received by two 'Olympus' strawberry plantings during treatment periods.

	1977 Planting		1978 Planting
	1st season	2nd season	1st season
	Irrigation period		
Irrigation regime[z]	July 21-Aug 22	July 7-Sept 7	July 7-Sept 7[y]
L	0	9.8	3.2
M	5.6	13.9[x]	13.9
H	17.2	29.1	29.1

[z] L, M and H denote low, medium and high irrigation regimes.

[y] This planting had rain shelters over the L and M regimes during most rainfall.

[x] Irrigation was adjusted such that the total included the 9.8 cm of rainfall.

Table 2. Effect of irrigation regime and poly mulch on the number of leaves and crowns per plant during the second season (1978) of the 1977 'Olympus' strawberry planting.

	Leaves/Plant		Crowns/plant	
Treatment[z]	July	September	July	September
L	58	89	14.1	16.7
LP	79	129	19.5	21.9
M	68	128	15.1	23.0
MP	88	170	20.3	24.9
H	83	159	16.0	22.0
HP	91	223	19.3	26.2
_F_ Tests				
Irrigation	NS[y]	***	NS	***
Mulch	*	***	***	***

[z] Low (L), medium (m) and high (H) irrigation treatments with or without polyethylene (P) mulch.

[y] *** = $p < .001$, * = $p < .05$, NS = $p > .05$.

Table 3. Regression relationships (R^2 values) for vegetative growth parameters of two 'Olympus' strawberry plantings.[z]

Variable			Year of Planting	
Dependent		Independent	1977	1978 (1)
October leaves	on	October crowns	.87 *** (1)[y]	.86 ***[x]
October plant size	on	October leaves + October crowns + cross product	------------	.89 ***
July leaf area	on	July leaf dry wt.	.97 *** (2)	.93 ***
July leaf dry wt.	on	July crown dry wt.	.65 *** (2)	.79 ***
July crown dry wt.	on	crowns in the previous October	------------	.65 ***
July leaf area	on	crowns in the previous October	------------	.87 ***
July leaf area	on	July crowns	------------	.31 NS

[z] All equations are simple linear regressions except plant size, which is a quadratic.

[y] Number (1) indicates data taken at or before the first fruit crop and number (2) is data at the second crop.

[x] *** = $p < .001$, NS = $p > .05$.

Table 4. Effect of irrigation regime and poly mulch on per plant leaf area, leaf dry weight, number of crowns, crown dry weight, and shoot/root ratio of 1 year old 'Olympus' strawberries (1978 planting).

Treatment[z]	Leaf area (cm^2)	Leaf dry weight (g)	Number of Crowns	Crown dry weight (g)	Shoot/root Ratio
L	4017	35.0	12.2	95.4	14.2
LP	5467	47.8	12.2	103.8	17.2
M	4199	36.5	16.2	98.1	15.7
MP	6838	54.9	15.8	124.5	19.3
H	5042	44.2	16.6	117.0	14.1
HP	6895	56.0	19.6	139.7	23.5
<u>F Tests</u>					
Irrigation	NS[y]	NS	*	NS	NS
Mulch	***	***	NS	**	**

[z] Low (L), medium (M) and high (H) irrigation treatments with or without polyethylene (P) mulch.

[y] *** = $p < .001$, ** = $p < .05$, NS = $p > .05$.

Table 5. Effect of irrigation regime and poly mulch on per plant leaf area, leaf dry weight, number of crowns, crown dry weight, and shoot/root ratio of 2 year old 'Olympus' strawberries (1977 planting).

Treatment[z]	Leaf area (cm^2)	Leaf dry weight (g)	Number of Crowns	Crown dry weight (g)	Shoot/root Ratio
L	3259	27.1	20.4	112.8	11.8
LP	4529	37.6	24.8	146.5	15.8
M	3847	30.2	27.0	159.2	10.7
MP	4202	34.9	27.4	160.9	14.4
H	3120	24.5	28.0	139.9	11.5
HP	4755	37.2	23.6	156.2	15.5
<u>F</u> <u>Tests</u>					
Irrigation	NS[y]	NS	*	NS	NS
Mulch	*	**	NS	NS	***

[z] Low (L), medium (M) and high (H) irrigation treatments with or without polyethylene (P) mulch.

[y] *** = $p < .001$, ** = $p < .01$, * = $p < .05$, NS = $p > .05$.

Figure 1. Summer pan evaporation (weekly totals) during 1977 and 1978. The treatments were begun 11 days earlier in 1978, and terminated as indicated by arrows on the abscissa.

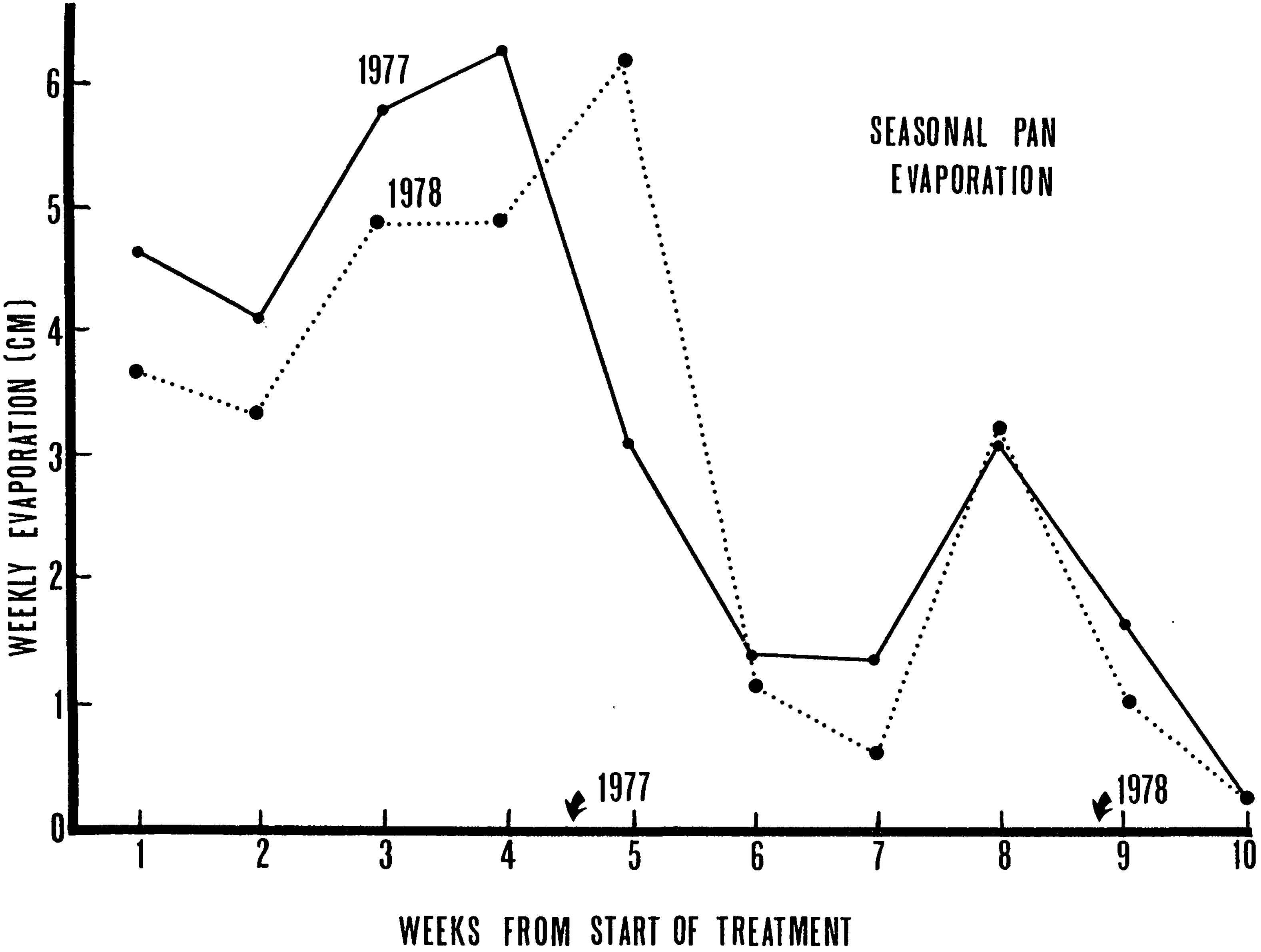

SEASONAL PAN EVAPORATION
1977
1978
WEEKLY EVAPORATION (CM)
0
1
2
3
4
5
6
WEEKS FROM START OF TREATMENT
1
2
3
4
5
6
7
8
9
10
1977
1978

Figure 2. Seasonal soil water potentials at 20 cm depth for the 1977 and 1978 plantings. The irrigation regimes were low (L), medium (M) and high (H), with or without polyethylene (P) mulch. The soil ψ for the H and HP treatments remained near 0 all season so the data for HP in 1978 and both H and HP in 1977 are omitted for clarity. Horizontal bars indicate periods of rainfall. The end of the main irrigation periods are indicated by arrows below the abscissa (August 22, 1977 and September 7, 1978).

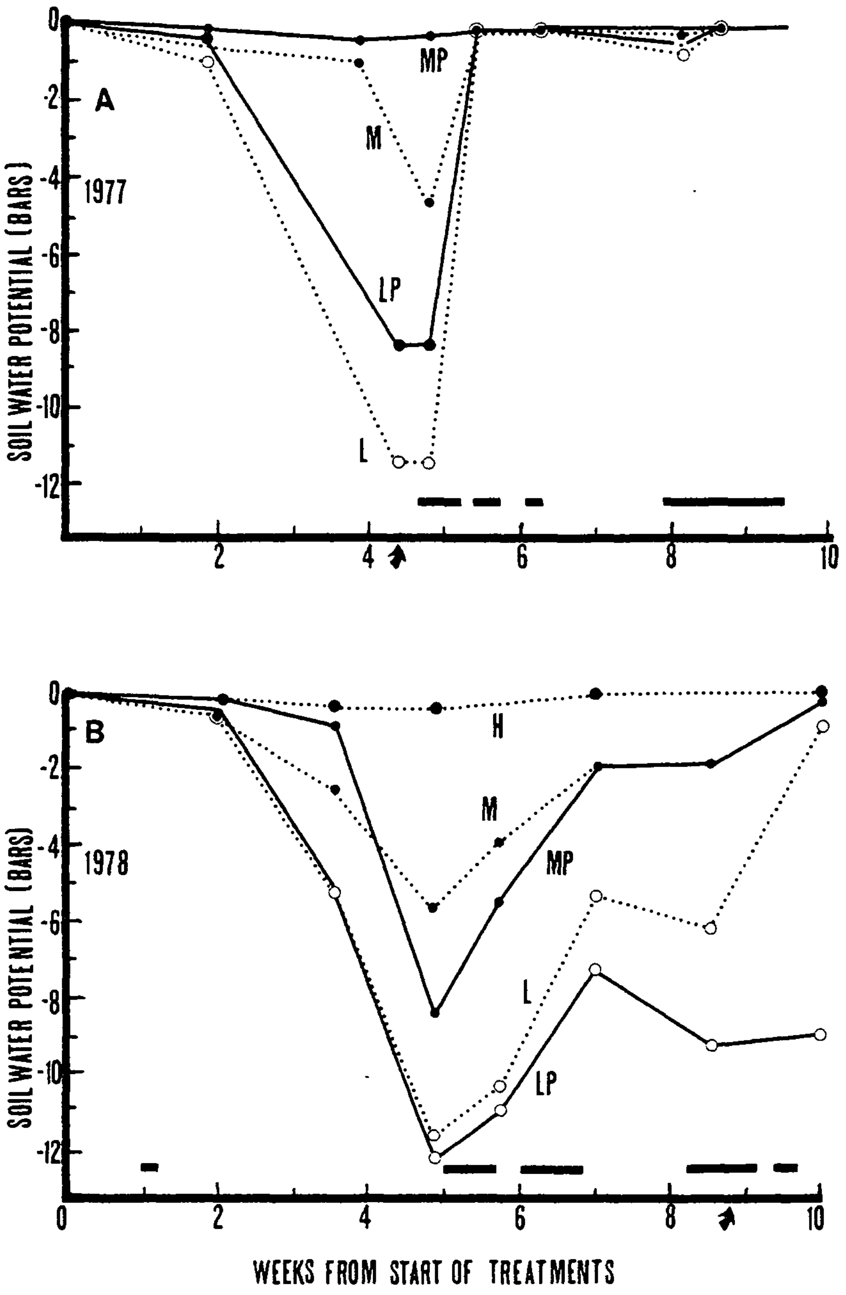
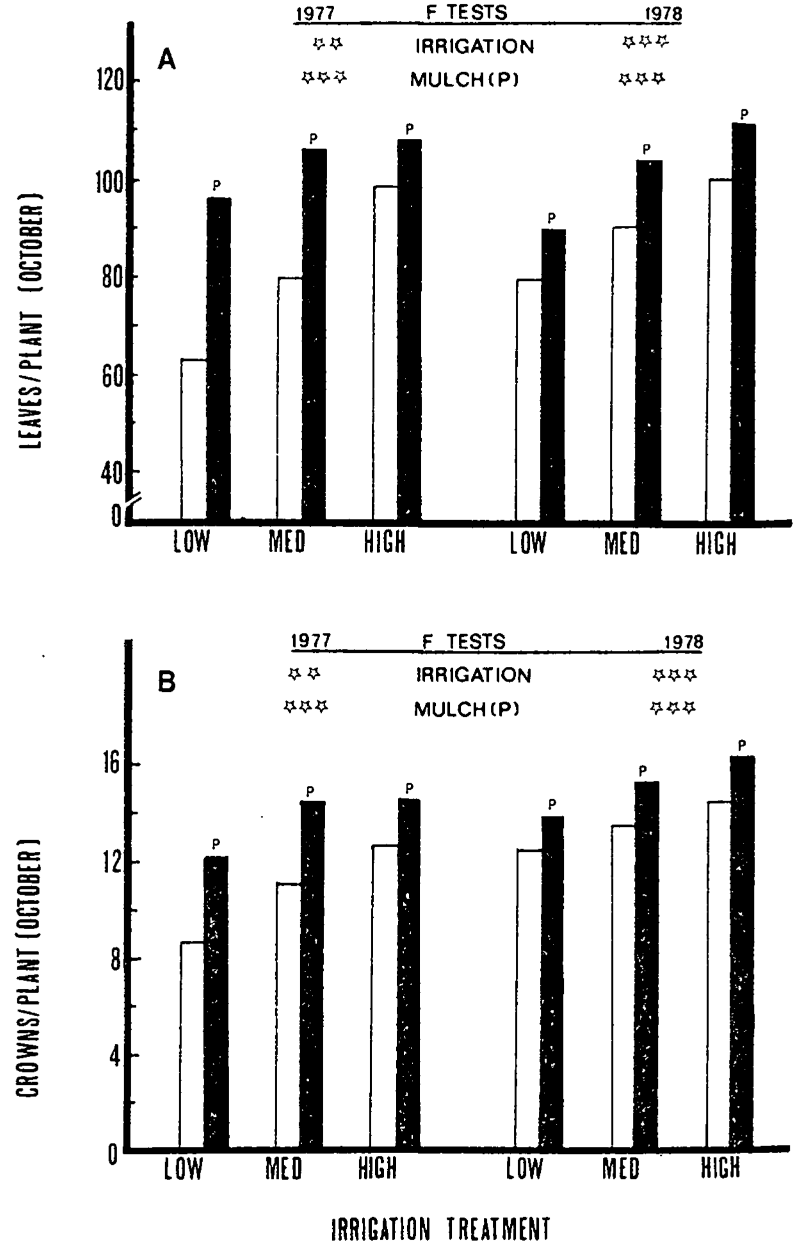

A
1977
0
-2
-4
-6
-8
-10
-12
SOIL WATER POTENTIAL (BARS)
MP
M
LP
L
2
4
6
8
10
B
1978
0
-2
-4
-6
-8
-10
-12
SOIL WATER POTENTIAL (BARS)
H
M
MP
L
LP
0
2
4
6
8
10
WEEKS FROM START OF TREATMENTS

Figure 3. The effect of irrigation regime and polyethylene (P) mulch on the number of leaves and crowns per 'Olympus' strawberry plant 5 months after planting. Irrigation rates for the Low, Medium and High regimes were 0, 0.23 and 0.70 of pan evaporation. The F test significance levels for irrigation and mulch are indicated (*** = $p < .001$, ** = $p < .01$).


1977 F TESTS 1978
✡✡ IRRIGATION ✡✡✡
✡✡✡ MULCH (P) ✡✡✡
A
LEAVES/PLANT (OCTOBER)
0
40
60
80
100
120
P
LOW
MED
HIGH
LOW
MED
HIGH
1977 F TESTS 1978
✡✡ IRRIGATION ✡✡✡
✡✡✡ MULCH (P) ✡✡✡
B
CROWNS/PLANT (OCTOBER)
0
4
8
12
16
LOW
MED
HIGH
LOW
MED
HIGH
IRRIGATION TREATMENT

EFFECT OF POLYETHYLENE MULCH AND SUMMER IRRIGATION REGIMES ON SUBSEQUENT FLOWERING AND FRUITING OF 'OLYMPUS' STRAWBERRY

A. Richard Renquist

Additional index words. *Fragaria x ananassa*, yield components, fruit size, drip irrigation

Abstract. Two field planting of strawberry (*Fragaria x ananassa* Duch. cv. Olympus) were grown at 3 rates of drip irrigation, with and without polyethylene mulch. Differential irrigation was applied only during 1 (1977) or 2 (1978) months during the summer. All treatments were irrigated equally during the following spring. In both summers the soil water potential at 20 cm depth was maintained above -0.3 bars for the highest rate of irrigation with mulch, and fell below -11 bars at the low rate without mulch. The highest irrigation regime had about 22% more flowers than the lowest in the spring of the first harvest season in both plantings. Mulch only increased flowering in the 1977 planting (12%), whereas the number of fruit was increased about 11% by mulch in both plantings. Irrigation caused a significant increase (20%) in fruit number only for the 1977 planting. The high yield capability of 'Olympus' was confirmed (37.8 MT/ha). Mulch increased the yield of the 1978 planting 18% despite its lack of effect on the number of flowers, suggesting a spring influence on yield. Irrigation did not significantly improve yield in 1978. In the 1977 planting the high and medium irrigation regimes both yielded 13% greater than the low regime, while mulch did not significantly increase yield that year. The second year crop of the 1977 planting yielded 26% lower than the first year, and failed to show

significant treatment differences in flower numbers or fruit yield, despite the much larger plant size with mulch and higher irrigation rates. The yield component which showed the greatest decline between years was the percentage fruit set. In general, mulch and greater summer irrigation increased fruit yield less dramatically than they enhanced vegetative growth, although mulch increased yield when irrigation was inadequate. Mulch also produced a greater water use efficiency.

Introduction

In a 1974 trial 'Olympus' strawberry produced 5 times the average fruit yield for Oregon when grown in raised beds with drip irrigation and black polyethylene mulch (13). Supplemental irrigation has often been shown to increase strawberry yields (6, 10, 15). Drip irrigation has not been clearly shown to improve strawberry yield in comparison to other methods (11, 14). In England either black or clear poly mulch increased strawberry production (1).

The vegetative response of the 'Olympus' to increased irrigation and poly mulch has been described previously (17). The fruiting response to these treatments is likely to be more complex due to the possibility of variable effects on the yield components at different phenological stages (8, 10, 15). The long time span between first season growth and fruiting could result in environmental modification of treatment effects. There is an increased likelihood of interaction between irrigation or mulch and factors such as plant age, plant size, and temperature (2, 3).

In the current study a range of drip irrigation regimes with and without poly mulch were examined to determine whether or not the vegetative growth responses in 'Olympus' were reflected in the flowering and fruiting performance.

Materials and Methods

The cultural system used in this study, the duration of treatments in each planting, the irrigation totals, and some key parameters of the growth environment have been described in detail earlier (17). Briefly, in 1977 and 1978 plants were spaced 38 cm apart and after establishment were drip irrigated at 3 rates referred to as low (L), medium (M) and high (H). Plants were established at uniform spacing in soil beds both with and without polyethylene (P) mulch. The 3 irrigation rates were 0, 0.23 and 0.70 of the depth of water evaporated from a Class A water pan. Differential irrigation was only in effect from July 18-August 19, 1977, and July 7-September 7, 1978. Clear poly rainshelters were in place over the L and M regimes of the 1978 planting during most rainfall in the 1978 treatment period. All treatments were irrigated equally at establishment and in the spring of fruit harvest years. Growth and fruiting data were recorded for 2 years on the 1977 planting and 1 year on the 1978 planting.

The reproductive growth data from 20 plants per treatment included the number of flowers and fruit, fruit size, and fruit yield were recorded in 1978 and 1979. In 1977 the fruit were counted and the number of flowers calculated from this by adding the number of undeveloped or atrophied blossoms, which were still distinguishable on the plant at the end of the fruit harvest. In 1978 the flowers were counted directly and the number of fruit calculated, using an average fruit size (weight) from a 25 berry subsample from each plot at each picking. In July of 1978 the first planting was harvested on 5 dates. In 1979 the harvest of both plantings was completed in 3 picking. Plants were dug following the 1979 harvest to measure leaf area and dry weights of plant parts, as described previously (17).

A split plot experimental design was used, with 6 treatment combinations (3 irrigation regimes with and without mulch), replicated 4 times. The objective of the analysis was to test the effect of mulch and the effect of increased irrigation, rather than make a 6 treatment comparison of all the combinations of these 2 factors.

Results and Discussion

Number of flowers and fruit. The components of strawberry fruit yield at a given plant spacing are the number of crowns, the inflorescences per crown, the flowers per inflorescence, the percent fruit set, and the average fruit size. A significant increase in the number of crowns due to mulch and increased irrigation was reported previously (17). The relative ranking of treatments in terms of crown number was the same at fruit-harvest time the following spring. Inflorescences were not counted since in 'Olympus' their low branching structure makes it difficult to obtain accurate counts on intact plants. The number of flowers and fruit were significantly increased in the first year of the 1977 planting both by mulch and by irrigation during the month long treatment period the previous season (Fig. 1). In these parameters, as well as all others in the study, the irrigation x mulch interaction was not significant. This supports a straightforward interpretation of the responses to the 2 treatments (increased irrigation and mulch) using the F-test from the split-plot Analysis of Variance table, rather than suggesting comparisons of 1 factor within each level of the other factor. Flowering in the 1977 planting was 21% greater at the high (H + HP) than the low (L + LP) irrigation rate, and was 12%

greater with mulch. The corresponding increases in fruit numbers was 20% and 10%. In contrast, the 1978 planting did not produce more flowers in response to mulch, though it did produce a 12% greater number of fruit. An increased supply of water during the 2-month treatment period the previous summer caused a 24% increase in number of flowers but a nonsignificant increase in number of fruit.

The different responses in the 2 plantings are probably explicable in terms of environmental effects on yield components. Understanding of such effects is incomplete, however. A major factor preventing enhancement of flowering by mulch in the 1978 planting was the greater number of flowers in the unmulched L and M treatments relative to the previous planting (Fig. 1A), such that the potential for a large positive effect of mulch was reduced. This was probably due to the greater number of leaves in the L and M treatments at the end of the first season in the 1978 compared to the 1977 planting (17), since flowering was closely associated with this measure of vegetative growth ($R^2 = .76$ for the linear regression equation, $p < .01$). Despite the differences between plantings, it is safe to conclude that both mulch and greater summer irrigation can increase subsequent production of flowers, with irrigation having the larger effect.

The number of fruit that develop is affected by factors in the spring, which may have contributed to the reduced effect of irrigation on fruit numbers compared to flowers in the 1978 planting (Fig. 1). The difference in fruit number between the 2 plantings is partly due to the method of calculation, but may also be attributed to adverse weather. In the first cropping spring for the 1977 planting many of the primary and some secondary fruit were absent or damaged, apparently due to frost. Removal of the dominant apical blossoms has been reported to enhance fruit set of the more numerous quaternary blossoms (19). The result could be an increase in fruit number, despite the loss of primary berries.

Fruit size. The average fruit size may also have been affected by the frost damage, since fruit from the first crop of the 1977 planting were small for all 6 treatments (averaging 5.5 to 6.0 g). Fruit were somewhat larger in the second crop of that planting (7.2 ± 0.2 g for all treatments), but significant treatment differences were again absent. The first crop of the 1978 planting, in contrast to the first year of the 1977 planting, not only included the large primary fruit but had conspicuously few small berries. Size ranged from 9.3 to 9.8 g with no mulch and 9.6 - 10.6 g with mulch. Fruit size was greater with mulch ($p < .05$) but not with added summer irrigation. The benefit of mulch on fruit size in the 1978 planting may have been due to higher soil and/or leaf and fruit temperatures in the spring. However, an effect of increased autumn temperature on early flower development is also possible (2), such as an increase in the number of achenes, which is a primary determinant of fruit size (9). The lack of improved fruit size from mulch in the 1977 planting may be a result of the high percentage of tertiary and quaternary fruit, which are more limited in size by potential number of achenes than springtime environment.

Fruit yield. The high yield capability of 'Olympus' was confirmed (37.8 MT/ha, see Table 1). Fruit yield was increased 13% in both years from the low (L + LP) to the high (H + HP) irrigation regime, but this was only significant for the 1977 planting (Table 1). Since the frost damage to the first crop of the 1977 planting is not typical, it can be concluded that increased summer irrigation does not significantly improve the fruit yield of the 'Olympus' strawberry. Mulch gave a highly significant 18% yield increase for the 1978 planting, but did not have a significant effect on the first crop of the 1977 planting. The percentage fruit set tended to be higher for mulched than unmulched treatments in the 1978 planting. In the 1977 planting fruit set was very high for all treatments, for reasons discussed above, so that there was probably less opportunity for mulch to enhance fruit set. The MP treatment had the top yield for both plantings, suggesting that when mulch was used the H rate of irrigation was excessive for fruit production, even though it resulted in the greatest number of leaves.

Second year responses. In the second year of the 1977 planting the number of leaves was increased 75% by summer irrigation and 39% by mulch, much greater gains than those from the first year (17). In contrast, the number of flowers per plant did not differ significantly due to treatment (Appendix Table 8-2), although all treatments equalled or exceeded the maximum flower number observed in the first crop (273 flowers per plant). The fruit set was quite similar among treatments, and the yields were not significantly different (Table 1). One cause of similar flower numbers despite large differences in vegetative growth may have been the early recovery of soil moisture levels in all treatments due to rainfall, since no rain shelters were used. Another consideration, discussed below, is that the plant size - fruit yield relationship may change as a plant ages (3).

Yield component relationships. The reproductive yield components nearly all showed significant linear regressions on each other and on those measures of vegetative growth where relationships were expected (Table 2). The components of fruit yield in strawberries have often been examined to interpret treatment responses and cultivar differences (4, 15, 20). The number of inflorescence-bearing crowns has been considered the key determinant of yield (7), and could explain the high yielding behavior of 'Olympus' compared to other cultivars in the Pacific Northwest. 'Olympus' crowns rarely lacked an inflorescence under Oregon conditions, in contrast to when it was grown at high latitude (20). Therefore, the total crown number is a useful index of yield potential in Oregon. The number of crowns in October for the 1978 planting was the single best independent variable on which to construct linear regressions of number of flowers, number of fruit, leaf area at fruiting time, and fruit yield (Table 2). For 1977 the use of the number of leaves in October was slightly better than crowns as the independent variable, though it is essentially a measure of the number of crowns, perhaps incorporating an element of crown size.

The number of developed fruit was a stronger function of the number of flowers in the 1977 than in the 1978 planting (R^2 = .89 vs. R^2 = .46), due to the more precise measure of fruit number in the former. Fruit set was also higher in the 1977 planting, perhaps because third and fourth order flowers, which were not frost damaged, had fewer achenes and were therefor less competitive. That may be why they developed into fruit as a more uniform function of the total number of flowers. In a favorable season, as experienced by the 1978 planting, the rapid enlargement of primary and secondary fruits may suppress fruit set of higher order berries, and the degree could vary with plant vigor or environment. This hypothesis, inferred from the work of Sachs and Izsak (19), could explain how fruit set is reduced by weather favorable to growth. An analysis by Ljones (12) of several years weather and fruiting data in Norway led to a related finding. In years when night temperatures during the month preceding fruiting were above average, the number of fruit was lower than the long term average. Fruit numbers (and perhaps fruit set) were therefore reduced by weather which is generally presumed to be more favorable to growth.

Fruit yield was more closely related to vegetative growth in the 1978 planting, despite the lower R^2 between flowers and crowns. The yield component with the greatest impact was the total fruit number. Fruit size had little effect, though in the year during which mulch increased fruit size there was a relationship of size to yield in the second of the 3 harvests (Table 2).

The 17% drop in fruit yield from the first to the second crop of the 1977 planting probably cannot be attributed to poor weather, and is not typical for 'Olympus' grown with standard cultural practices (13), although a decline did occur in the previous trial with drip irrigation and mulch (Martin, unpublished). In terms of yield components, the decrease occurred despite a large increase the second year in the number of crowns, leaves, and flowers, and a 26% greater average fruit size. All of these were apparently offset by a sharp drop in the percentage of fruit set, resulting in fewer fruit per plant on an absolute basis. An average of 44% of the flowers developed into harvestable fruit in the second year, compared to 76% for the previous crop and 61% for the 1978 planting (with the same environment and counting method). Yield component relationships are known to change with plant age. In Scandanavia increasing crown development is often accompanied by increasing yield until the second or third year (3). In the Pacific Northwest 'Olympus' and some other cultivars produce equally large crops the first 2 years, and then may decline. Perhaps the drip irrigation and mulch combination promotes such rapid crown branching the first season that additional fruiting sites created in the second year are in excess of what can be supported. Further increases in plant size with irrigation or mulch would therefore fail to enhance yield and could be counterproductive. In an earlier Oregon study summer irrigation of established plantings also increased plant growth with little effect on fruit yield (16).

Leaf area is a factor which may help explain why the second crop was actually reduced and not merely equal to the first crop of the 1977 planting. As noted in the previous paper (17), the 2 year old plants had considerably more leaves in July, yet total plant leaf areas averaged 27% less than on the corresponding 1 year old plants. The leaf area per crown was an average of 56% lower in 2 year old plants, creating a possible limitation on photosynthate supply per inflorescence. Strawberries may be fairly sensitive to reduced leaf area, since the leaf area indices at harvest time for the 38 cm spacing used are only 1.4 - 2.4, even when one third of the soil surface (the access aisle) is excluded. However, the mulched treatments had 29% greater leaf area per crown but did not yield higher.

Another aspect of plant structure that should be considered is the root system, since we detected no treatment effect on root dry weight for either 1 or 2 year old plants (17), although shoot dry weights differed greatly. The single small root system could have contributed to the lack of differences of the second fruit crop, and also reduced the range of yields of the first crop for a low runnering cultivar like 'Olympus'. The reduced fruit yield the second year cannot be readily ascribed to the root dry weight, since it was greater for the 2 year old plants, and shoot/root ratios were lower.

The fruit yield per plant based on the bulk yield of the highest yielding treatment was 61% greater than in the previous irrigation and mulch trial with 'Olympus' (13). The very high yield in that trial (53 MT/ha) resulted from a plant population of 65,200 plants/ha, compared to 24,700 plants/ha used to calculate the yields given here. Smaller plant size would be expected at higher density, but the yield increase from the added plants would probably not be offset by the reduced per plant yield, since the largest plants in the present study (HP) only yielded 24% higher than the smallest plants (L). The optimum spacing of 'Olympus' has yet to be established.

Conclusions

The results suggest that while polyethylene mulch and increased summer irrigation both strongly promote vegetative growth, their effects on fruit production are less dramatic. Mulch can appreciably increase the first year yield of 'Olympus' when irrigation is inadequate, and tends to increase the size (dry weight) of plant parts, while both irrigation and mulch increase their rate of production. Further examination of yield component relationships between the time of floral initiation and fruiting is needed, as is a better understanding of environmental influences on such components as fruit set and fruit size. Since yield was reduced when vegetative growth was too greatly suppressed by a water deficit, an additional study examined leaf growth in relation to leaf water status (18) to characterize aspects of the physiology of drought response in strawberry.

In terms of water use efficiency the conclusions drawn from the yield data (Table 1) are the same as those for vegetative growth (17). Namely, mulch plus summer irrigation at the M rate, whic is low compared to standard rates of sprinkler irrigation on sandy loam soil (6), out-yielded any of the unmulched treatments. Whether the mulch effect is due to direct soil moisture conservation or an indirect enhancement of growth at higher temperatures, the result is an improved water use efficiency.

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Table 1. Effect of summer drip irrigation regime and polyethylene mulch on fruit yield for 2 'Olympus' strawberry plantings.

	1977 Planting				1978 Planting	
	1st Crop		2nd Crop		1st Crop	
Treatment[z]	g/plant	MT/ha	g/plant	MT/ha	g/plant	MT/ha
L	903	22.3	883	21.8	1126	27.8
LP	1043	25.8	770	19.0	1294	32.0
M	1054	26.0	874	21.6	1114	27.5
MP	1149	28.4	854	21.1	1531	37.8
H	1104	27.3	755	18.6	1336	33.0
HP	1089	26.9	862	21.3	1401	34.6
<u>F</u> <u>Tests</u>						
Irrigation	*[y]		NS		NS	
Mulch	NS		NS		**	

[z] Low, medium and high irrigation regimes = L, M and H, with or without polyethylene (P) mulch.

[y] ** = $p < .01$, * = $p < .05$, NS = $p > .05$.

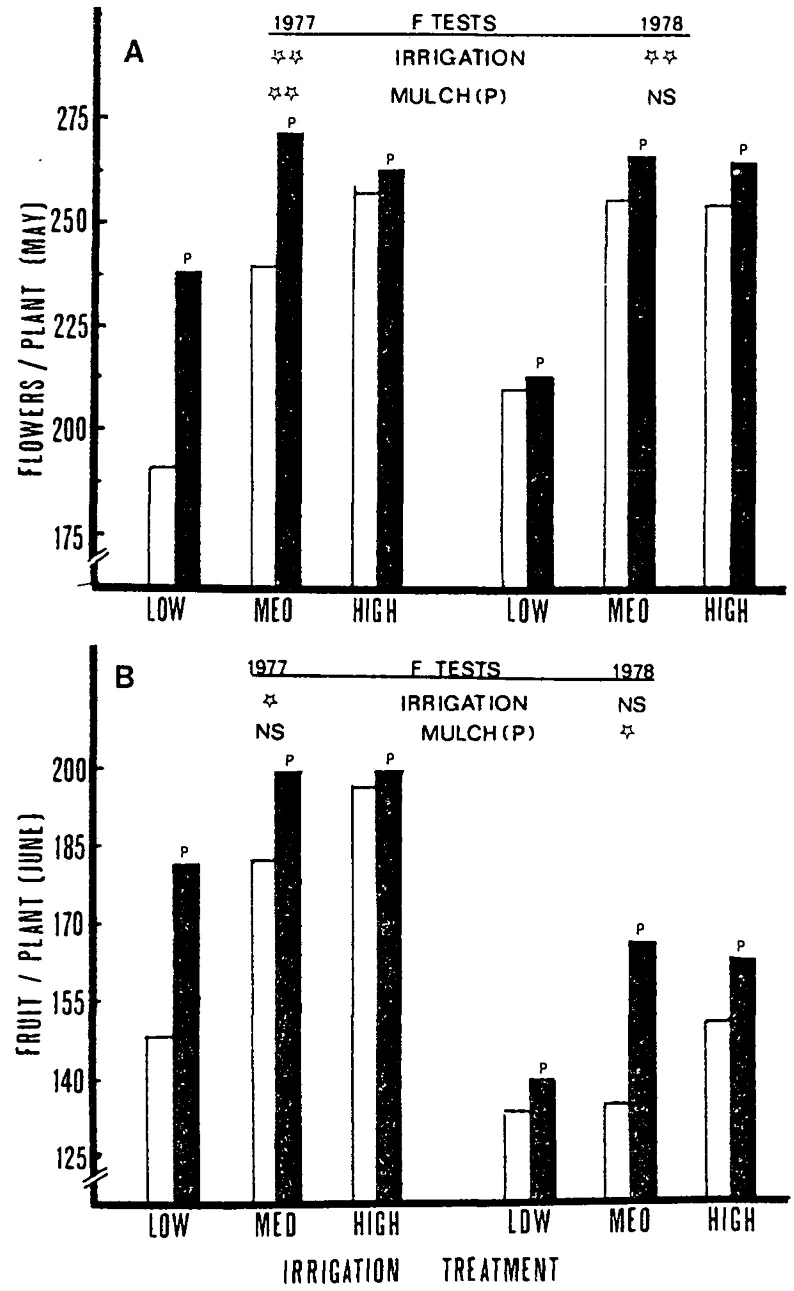
Table 2. Linear regression relationships (R^2 values) for vegetative and reproductive growth parameters in the first year of two 'Olympus' strawberry plantings.

Variable				
Dependent		Independent	1977 Planting	1978 Planting
May Flowers	on	October 77 Leaves/[z]	.65 ***	--------
		October 78 Crowns	--------	.49 ***
Total Fruit	on	October 77 Leaves	.56 ***	--------
		October 78 Crowns	--------	.57 ***
Fruit Yield	on	October 77 Leaves	.37 **	--------
		October 78 Crowns	--------	.57 ***
Fruit Yield	on	Current Leaves	.33 **	--------
Total Fruit	on	Flowers	.89 ***	.46 ***
Fruit Yield	on	Flowers	.75 ***	.31 ***
Fruit Yield	on	Total Fruit	.80 ***	.84 ***
Fruit Yield	on	Fruit Size	NS	NS
Fruit Yield	on	Fruit Size (2nd picking)	--------	.35 **

[z] Leaves were the preferred independent variable of vegetative growth in 1977, while crowns were better in 1978.

[y] *** = $p < .001$, ** = $p < .01$, * = $p < .05$, NS = $p > .05$.

Figure 1. Effect of summer irrigation regime and mulch on the number of flowers and fruit per plant in the first crop of 'Olympus' strawberries planted in 1977 and 1978. Irrigation rates for the L, M and H regimes were 0, 0.23 and 0.70 of pan evaporation. The F test significance levels for irrigation and mulch are indicated (** = $p < .01$, * = $p < .05$, NS = $p > .05$).


A
1977
F TESTS
1978
☆☆ IRRIGATION ☆☆
☆☆ MULCH (P) NS
FLOWERS / PLANT (MAY)
275
250
225
200
175
P
LOW
MED
HIGH
LOW
MED
HIGH
B
1977
F TESTS
1978
☆ IRRIGATION NS
NS MULCH (P) ☆
FRUIT / PLANT (JUNE)
200
185
170
155
140
125
P
LOW
MED
HIGH
LOW
MED
HIGH
IRRIGATION TREATMENT

INFLUENCES OF WATER STATUS AND TEMPERATURE ON LEAF ELONGATION IN STRAWBERRY

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Additional index words. *Fragaria x ananassa*, water potential, osmotic potential, cell expansion, osmotic adjustment

Abstract. Well irrigated (IR) and non-irrigated (NIR) strawberries (*Fragaria x ananassa* Duch. cv. Olympus) were compared in terms of water potential (ψ), solute potential (ψ_s), turgor potential (ψ_p), and leaf elongation rate (LER) during diurnal cycles in a greenhouse and the field in 1978-1979. LER increased with ψ_p under relatively constant day and night greenhouse temperature. In the field LER was maximal during a 5-hr period beginning 1 hr before sunset. Low leaf temperature (below 16-18°C) apparently limited LER during the remainder of the night until mid-morning, and low ψ_p was probably the limiting factor in the afternoon. In 1978 leaflet length was measured daily from 13 to 27 days after the start of differential irrigation. The mean LER during the first week was 52% higher and the final area of the center leaflets averaged 85% greater for IR than NIR plants. In 1979, after 62 days of irrigation treatments, the total leaf area of IR plants was 205% greater, which was the combined effect of greater leaf size and number. The average LER was determined during 3 days in growth chambers at 10, 15, 22 and 28°, and was maximal at 28°. After 2 weeks in the 28°

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[1] The generous equipment loans by L. H. Fuchigami and L. Boersma are gratefully acknowledged.

chamber the LER of new leaves declined, however, suggesting that 28° was supra-optimal for strawberry. Osmotic adjustment, an adaptive response to water deficit, increased ψ_p at a given ψ in NIR field-grown strawberries but did not appear to prevent a reduction in LER. The adjustment failed to occur in the greenhouse-grown plants, presumably due to the low light level during winter. The practice of measuring LER on a young leaf while estimating its ψ_p by measuring ψ and ψ_s on larger leaves appears questionable for field-grown strawberries. The assumption of uniform ψ_s should be tested.

Introduction

In an earlier study (19) we found that if leaf growth of strawberry was too greatly suppressed by a water deficit during the first summer the subsequent fruit yield was reduced. We, therefore, initiated a study to examine the influence of water status on strawberry leaf expansion. The role of temperature, which is often a major influence on leaf expansion (24), was also studied.

It is commonly recognized that strawberry leaf size is reduced by water deficit, however the effects have not been quantified or related to leaf water status. It is also recognized that much of the leaf growth in strawberry occurs early in the spring and must therefore be less inhibited by low temperature than in a crop like maize (2, 5). To make a real comparison however, it is necessary to quantify the temperature responses of strawberry. In addition, to correctly characterize leaf elongation in terms of water status and temperature requires awareness of other influences which must be held constant, such as nutrition and daylength. It has been shown that longer days increase the duration of cell expansion and therefore the final leaf size (1).

The basic equation used to describe the rate of cell growth is $G = E\ (\psi_p - \psi_{p_{TH}})$, where E is the extensibility coefficient, ψ_p is the pressure potential or turgor, and $\psi_{p_{TH}}$ is the threshold turgor required for any enlargement to occur (18). Turgor is probably the only driving force for cell and leaf expansion since neither has been observed to occur at zero ψ_p. Yet is can only control the LER when other factors such as low temperature (3) and hormone levels (11) are non-limiting.

A close linear relationship of LER to Ψ_p, as found in soybean (9), is most likely to exist in the field when night temperature is moderately high. A small drop in ψ_p rapidly reduces the short term rate of elongation, although recovery often occurs without restoring the original ψ_p (27). Leaf expansion over a few hours or days is sensitive to mild stress in a wide range of crops (7, 14, 15, 16). Long term reduction in leaf area has also been correlated with water deficit (17).

We compared the leaf elongation rates in irrigated and non-irrigated strawberries and described the influences of turgor potential and temperature in the field and in a greenhouse. Differences in the relationship between water status and growth due to environmental factors such as light level and soil rooting volume could therefore be assessed.

Materials and Methods

'Olympus' strawberry plants weighting 9-18 g with roots trimmed to 10 cm were established in 3- liter pots in a greenhouse. The media was a 3:1 mix of soil and peat, fertilized as needed with soluble 30-4-8 NPK. In the greenhouse sodium vapor lights provided a 15 hr photoperiod, which promotes vegetative growth and prevents floral initiation. Greenhouse data were collected in the fall, winter and spring from plants with midday photosynthetic photon flux densities (PPFD, from 400-700 nm by definition) ranging from 120-200 $\mu E\ m^{-2}s^{-1}$ in December to 250-1400 $\mu E\ m^{-2}s^{-1}$ in the spring and fall. Since these represented much of the range between the minimum light level used and that in the field (2000 $\mu E\ m^{-2}s^{-1}$), it was possible to determine the effect of light level on 1 aspect of the water status, the ψ_s. Temperature was 18°C at night and 21-32° maximum in the day. Old leaves were removed so that plants had a uniform canopy of 7-10 expanded leaves and several younger ones at the start of each experimental period. Water was withheld from two-thirds of the plants for 4 days prior to the start of measurements. Plants were selected from this NIR group on the basis of uniform leaf ψ since the rate of stress development (decline in ψ) varied once water was withheld.

The field studies were made with first year plantings, using drip irrigation and raised beds of fertile sandy loam soil (19). The dates of the experimental periods and environmental data are listed (Table 1). Leaf canopy temperature was recorded on September 6, 1979 with an infrared thermometer (Barnes IRT-2) calibrated using a black body cavity. Concurrent measurements of LER, leaf ψ, ψ_s, and relative water content (RWC) were made every 5-8 hours during experimental periods. Data was from at least 5 IR and 5 NIR plants, both in the field and in indoor environments. In the greenhouse the required excision of leaves for ψ determination at each sampling time left only 3 plants per treatment for measuring LER at the final sampling. ψ_p was calculated as ψ minus ψ_s, assuming matric potential to be negligible (6). The unit used for ψ and its components was bars (1 bar = 10^5 Pascals).

LER was determined by periodic measurement of the recently unfolded center leaflet of a tagged trifoliolate with a ruler. Leaflets were usually 30-35 mm at the start of each experimental period and pre-selected as representative of the treatment population. Maximum LER was from 30 to 70 mm, which is similar to the elongation behavior of soybean (9). The final area of each leaflet was measured on an electronic area meter and a conversion factor established for the leaflet length x width product. These ranged from .60 - .64 and did not differ due to treatment. Leaflet lengths from the 1978 field study were converted to area by the lenear regression equation: area (cm^2) = .735 length - 32.15, which was developed with data from xerographed leaves ($R^2 = .93$). This also did not differ with treatment. Nearly instantaneous LER's were recorded for periods of several hr using a linear variable differential transducer (LVDT) (4). Petioles were fixed in place during these short term measurements so that only leaf lamina growth was recorded.

Leaf ψ was estimated with a pressure chamber (28) which measures xylem pressure potential. The xylem sap was very low in solutes, a requirement for an accurate estimate of ψ. Prior removal of lateral leaflets for ψ_s and RWC determination did not affect the measurement of ψ significantly.

ψ_s was measured with a Wescor dewpoint hygrometer (7) on leaf sap. A single leaflet was removed from the trifoliolate and frozen on dry ice in the field or greenhouse, then stored at -60°C. The leaflet was allowed to thaw for 40 min. prior to expressing the sap. This method probably overestimates ψ_s since the symplastic water of burst cells is mixed with the dilute apoplastic water in cell walls (5, 27). This error is detected when values of total ψ are lower than ψ_s i.e., leaf turgor (ψ_p) appears negative. Such was the case with strawberry, so an adjustment of 10% was made on all ψ_s data, based on the findings of Boyer and Potter (5) and Wenkert (29).

The RWC was determined on 8-10 leaf discs 8 mm in diameter from a leaflet which had been excised and held in a sample bag in a cooler. The method of Weatherley was followed, with modifications (21).

The temperature response study utilized growth chambers at 10, 15, 22 and 28°C, with a PPFD of 360-480 $\mu E\ m^{-2} s^{-1}$. The length of 5 leaflets per chamber was measured twice daily starting 3 days after plants were placed in the chambers. All plants were well watered. Single leaves were attached to an LVDT to compare short term LER at different times of the day and night. During 2 days the entire system (i.e., the plant, LVDT apparatus, and recorder) was moved as a unit from the 22° chamber to either the 15° or 28° chamber and back again, to record the shifts in LER.

Results and Discussion

Leaflet length was measured once or twice daily for 29 days beginning July 28, 1978, 13 days after the start of irrigation treatments. While leaves of IR strawberry plants doubled in length in 7 days, those on NIR plants showed a 65% increase (Fig. 1). This represents a 52% higher mean rate of elongation in IR plants. There was a lack of growth by NIR plants during the daytime interval on some days, while IR plants grew approximately equally during the day and night periods. This has also been observed in leaves on NIR potato plants (14). The leaflet length after 14 days was 20% higher for IR plants, which is equivalent to an 85% greater leaf area. Measurements during an additional 15 days showed that the leaflet area in the IR treatment was only 35% greater than NIR leaflets as they approached their final sizes. Reduced evaporative demand appeared to be a prerequisite for the increase in growth rate which occurred in NIR leaflets. A month later it took 11 days rather than 7 for the IR leaflets to double in length from the same initial size, probably due to the reduced day length (1). In a 1979 planting, with less summer rainfall, the total leaf area of IR plants after 62 days of treatments was 205% greater than NIR, which was the combined effect of greater leaf size and number.

The LER of IR strawberries was greater than that of NIR plants in both the greenhouse and field. During each 8-hr interval in the greenhouse experiment leaflet elongation of NIR plants was half that of IR plants (Table 2). In all experiments the variability in elongation was much greater in the day than at night, suggesting that it was due to variation in the micro-environment of the leaves. Mean separation between IR and NIR plants equalled or exceeded 2 standard errors only during the night. Much larger sample sizes would be preferable, although the relative responses to the IR and NIR treatments can be discerned from the means. When comparing the elongation of leaflets over the final 24 hr period before each was excised, the treatment means were more distinct. The increase was 4.5 ± 1.4 mm for IR and 2.0 ± 0.6 mm for NIR greenhouse plants.

A reduction in LER in NIR compared to IR crops is usually ascribed to reduced ψ_p (15). Tables 2 and 3 include complete ψ and ψ_s

data used to calculate ψ_p in the greenhouse and field, respectively. LER was compared to the mean ψ_p, based on the initial and final values for each 8-hr interval in the greenhouse (Table 4). A positive influence of increasing ψ_p on LER was apparent, although a precise mathematical relationship could not be determined. To do so would require a more sensitive system for LER measurement as well as integrated measurements of ψ_p and temperature.

Several investigators (3, 25) were unable to even roughly characterize the LER of maize on the basis of ψ_p when day and night temperatures varied greatly. A multiple regression of LER on ψ_p and temperature was successful, however (2). We therefore determined the effect of temperature on strawberry LER and petiole elongation rate (PER) in 4 growth chambers from 15° to 28° (Fig. 2), in order to compare the response to that of maize. The 72 hr mean PER, starting 3 days after plants were placed into the growth chambers, was very temperature sensitive and increased exponentially across the whole 10° to 28° range tested ($Q_{10} = 2.5$). The elongation rate of a leaflet, measured with an LVDT, rapidly increased from .15 to .32 mm hr^{-1} when the plant was moved from 22° to 28°, but decreased from .16 to .06 mm hr^{-1} when moved from 22° to 15°. In both cases the initial rate was restored within minutes when the plant was returned to the 22° chamber. The maximum long term LER (over 72 hr starting on the third day of temperature treatments) also occurred at 28°. However, LER increased most rapidly between 15° and 22°, and the optimum for leaf elongation may have been between 22° and 28° (Fig. 2). The possibility that 28° was supra-optimal was suggested by follow-up measurements of LER after plants had been in the chamber for 2 weeks. Here, the 3 day average LER was greater at 10° and 15° but lower at 28° than in the above-mentioned 72 hr period (data not shown). The temperature responses in short-term and less-acclimated situations may not reflect the differences between species with respect to leaf growth adaptation to low or high temperatures. The reduced strawberry LER after two weeks at 28°, and probably the increased LER at 10° and 15°, would be unlikely responses for maize. Yet strawberry reacted to temperature much like maize (24) during short-term measurements of LER.

The diurnal pattern of LER for both IR and NIR strawberries on August 31, 1979 in the field was apparently influenced by temperature (Table 5). For both treatments, LER was maximal between 1800 and 2300 (sunset occurred at 1850), and it was low the remainder of the day. LER measurements of IR plants were made during the same time intervals on a similar day a week later (September 6), with concurrent measurement of ψ_p and leaf canopy temperature. The mean leaf temperatures were within 1°C of mean air temperatures, so that the earlier diurnal pattern of LER (Table 5) can be interpreted in terms of air temperature. The data suggests that temperature was the major limitation on LER from 2300 - 0800, since ψ_p is nearly always maximal at that time, as was found on September 6 (Table 5). During the period of minimum LER (0800 - 1300) growth may have been inhibited by the 2 factors in sequence, first low temperature and then low ψ_p. The rapidly elongating leaves of maize allow frequent measurements and therefore finer detail in the course of LER. As a result Acevedo (2) was able to isolate short segments of the time course where temperature influences on LER accounted for > 90% of the sum of squares in a multiple regression, and other time segments where ψ_p was equally predominant. Identification of such intervals for the slowly-elongating strawberry leaves would have required a more sophisticated field device for LER measurement, such as that used on soybean by Wenkert (27).

The leaf expansion strategy of strawberry in an area with cool summer nights, such as western Oregon, appears to be based on a short period of relatively rapid growth, starting near sunset and lasting 3-5 hr. This was most apparent for NIR plants (Table 5), where elongation from 1800 - 2300 was greater than for the other 18 hr combined. A period of maximum elongation near sunset has been reported for at least 5 other species (16). What is probably an important component of this strategy for strawberrry is the diurnal pattern of stomatal movement, described in detail elsewhere (20). Stomata were nearly closed by 1700 in the field, probably due to decreasing light. This may have been a circadian rhythm, since closure had begun 2 hr before lights went off in a growth chamber study (20). As a result of this stomatal closure ψ_p is able to recover rapidly due to reduced transpiration. At this time temperature is still favorable for rapid growth and the level of accumulated photosynthate is probably maximal. The soil moisture level is also crucial since ψ_p recovered faster in IR plants even though their stomata closed more slowly.

The relationship between LER and water status differed greatly in the greenhouse vs. the field environment. The primary factor, temperature, was considered above. It was shown elsewhere (20) that diurnal leaf ψ became progressively lower in NIR than in IR plants in the greenhouse. In the field only slight treatment differences occurred, even after 5 to 6 weeks (20). The 2 greenhouse environmental factors which contributed to this difference from the field were the small soil volume in pots, which resulted in lower ψ in greenhouse vs. field NIR plants, and the lower solar radiation, which resulted in higher ψ in greenhouse vs. field IR plants. Since these factors altered leaf ψ in opposite directions, it is apparent that the effect of soil volume must be predominant for NIR plants. Irrigation treatment differences in ψ_p, as in ψ, were also distinct in the greenhouse (Table 2) and were absent in the field (Table 3). This was primarily due to the greater soil water depletion in pots, but also resulted from the lower light levels in the greenhouse than in the field, which reduced the degree of adaptive ψ_p maintenance. This adaptive response resulted in very similar ψ_p in the field even on days when ψ was lower in NIR plants (Table 3). The mechanism, called osmotic adjustment, involves an active accumulation of solutes that lowers ψ_s and increases ψ_p at a given ψ by inducing water movement into cells (3). The degree of adjustment may depend on the overall ability to accumulate solutes (usually carbohydrates or organic acids) in a given environment. Predawn ψ_s in the field (see 20, Table 2) was -18.8 bars for NIR plants, compared to -14 bars in leaves of the same age on more severely stressed plants in the greenhouse in December. Since this is the reverse of what would be expected in terms of osmotic adjustment to water deficit, it appears that the mechanism is limited in the greenhouse environment. A comparison in the greenhouse of ψ_s to PPFD for both IR (Fig. 3) and NIR (not shown) strawberries indicated that low light (below 500-800 $\mu E\ m^{-2}s^{-1}$) reduced the midday decline in ψ_s. This effect was previously mentioned by Watts (25).

Since ψ_p differed between treatments in the greenhouse, but not in the field, LER of IR plants might also be expected to exceed that of NIR plants in the greenhouse but not in the field. As previously stated, however, the LER of IR strawberries was greater in both environments. Long term LER in the field based on final leaf size, was also greater in IR plants. Two considerations may help explain these anomalies in the field data. When water status was compared (Table 3; ref. 19, Table 2), IR plants frequently had higher leaf ψ but rarely higher ψ_p than NIR plants. Therefore ψ_p was equal in the 2 treatments only as a result of osmotic adjustment. While such adjustment has been credited with sustaining midday leaf elongation in sorghum (15), in rice it was found that LER was reduced despite the maintenance of Ψ_p (12). Strawberry may respond like rice in this respect. The second consideration, concerning the reduced long term LER in NIR strawberries, is that this behavior has been widely reported, even in crops which maintain a high midday LER during drought (15). The causes of this are unknown. A recent analysis of rice LER (13) indicated that it may be less closely related to ψ_p, per se, than to the fluxes of water, as controlled by ψ gradients in the plant. The fairly direct relationship of LER and ψ_p for greenhouse strawberries may be artificial since osmotic adjustment was absent. More study of LER vs. water status in the field is clearly needed.

Mention should be made of leaf age as a possible source of error in interpreting the relationship between LER and ψ_p. A leaflet

30-40 mm long was insufficient tissue for ψ_s determination, so that in some of these studies and others reported in the literature a larger adjacent leaf was removed and measured simultaneously with leaflet elongation. The ψ_s was assumed to be equal for the 2 leaf sizes, and a test in the greenhouse showed this to be valid within 2 bars. In the field, however, leaflets which were just large enough to measure (65-70 mm long) had an average midday ψ_s 4.3 bars higher than fully expanded leaflets approximately 2 weeks older. The ψ_s of very young leaflets may have been higher yet. Turgor of the young expanding leaves was therefore overestimated by a considerable amount. It appears that the assumption of uniform ψ_s should be tested before it is relied upon in characterizing the water status-growth relationships of a species.

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Table 1. Starting dates and environmental data for studies of water status and temperature influences on strawberry leaf elongation. Locations were in the field (F), greenhouse (GH), and growth chamber (GC).

Starting Date	July 28, 1978	July 31, 1978	August 31, 1979	December 20, 1978	May 29, 1979
Location	F	F	F	GH	GC
Photoperiod (hr)	14.5	14.5	13.3	15	15
Max. Temp. (°C)	30[z]	26.5	26	23	10, 15, 22, 28
Min. Temp. (°C)	13[z]	11	13	19	same as max.
Midday light (μE m^{-2} s^{-1})	1500-2200[z]	2000	1500-1750	120-180	360-480
Pan evaporation (cm)	0.70[z]	0.58	0.05	--	--
Days of differential irrigation[y]	13	16	42	4	0
Days of measurement period	29	1	1	1	3

[z] The average for the 14 days shown in Fig. 1.

[y] Prior to the start of measurements.

Table 2. The dirunal course of leaf water potential (ψ), solute potential (ψ_s), turgor potential (ψ_p), relative water content (RWC) and increase in the center leaflet length (ΔL) in irrigated (IR) and non-irrigated (NIR) strawberries in a greenhouse starting December 20, 1978. The photoperiod was from 0700-2200.

Time	1400		2200		0600		1400	
Treatment	IR	NIR	IR	NIR	IR	NIR	IR	NIR
ψ (bars)	- 5.0±0.4[z]	- 9.4±1.5	- 2.4±0.2	- 7.8±4.4	- 2.4±0.4	- 8.2±2.0	- 6.2±0.4	-13.1±2.8
ψ_s (bars)	-11.9±1.2	-15.0±1.0	-12.5±1.5	-13.2±1.9	-10.8±1.0	-12.2±1.1	-11.5±0.6	-14.4±1.2
ψ_p (bars)	6.9±0.9	5.3±2.0	10.1±1.6	5.4±1.9	8.4±1.2	4.0±1.3	5.3±0.7	0.9±1.8
RWC (%)	---	---	93.2±1.3	88.2±5.8	95.2±0.2	90.0±2.1	89.4±1.7	82.3±3.5
ΔL(mm)	---	---	1.2±1.1	0.6±0.5	2.0±0.0	1.0±0.0	1.3±1.0	0.5±0.7

[z] ± SE

Table 3. Diurnal leaf water potential (ψ), solute potential (ψ_s), and turgor (ψ_p) in irrigated (IR), and non-irrigated (NIR) strawberries in the field starting July 31, 1978, which was the third day of the leaf growth experiment in the same planting (Fig. 1). See Table 1 for weather data.

Time	1500		2100		0530	
Treatment	IR	NIR	IR	NIR	IR	NIR
Ψ (bars)	-15.3±2.7[z]	-15.5±1.8	-3.7±0.6	-6.0±1.2	-1.2±0.4	-3.0±0.7
Ψ_s	-17.6±1.2	-19.1±0.9	-15.2±1.2	-16.9±0.7	-13.6±0.9	-15.9±1.7
ψ_p	2.3±2.8	3.8±2.1	11.6±0.9	10.9±1.0	12.4±0.8	12.9±1.0

[z] ±SE

Table 4. Leaf elongation rates (LER) of irrigated (IR) and non-irrigated (NIR) greenhouse-grown strawberries and average turgor potential (ψ_p) during each of 3 8-hr intervals starting on December 20, 1978. See Table 1 for environmental details.

Time	1400-2200		2200-0600		0600-1400	
Treatment	IR	NIR	IR	NIR	IR	NIR
Ave. ψ_p (bars)	8.5	5.3	9.3	5.2	6.9	2.5
LER (mm hr^{-1})	.15±.14[z]	.08±.07	.25±.06	.13±.06	.16±.12	.06±.09

[z] ±SE

Table 5. Leaf elongation rates of irrigated (IR) and non-irrigated (NIR) strawberries during 23 hr in the field, starting at 0900 on August 31, 1979.

Time Interval	Mean air temp (°C)	Mean ψ_p (bars)[y]	LER (mm hr^{-1})	
			IR plants	NIR plants
0900-1300	21.5	7.0	.10±.13[z]	0
1300-1800	25	6.8	.18±.17	.05±.09
1800-2300	20.5	9.4	.43±.07	.20±.11
2300-0800	16	10.1	.14±.05	.04±.06
Overall	---	----	.20±.06	.07±.03

[z] ±SE

[y] Data for IR plants on September 6, 1979 to illustrate mean ψ_p values for the various time periods.

Figure 1. Strawberry leaflet elongation for irrigated (IR) and non-irrigated (NIR) plants during 14 days in the field starting July 28, 1978. Leaflet length of IR plants had doubled by the date indicated with an arrow. Standard errors are shown on 3 randomly-chosen dates. The daytime interval, 0700-1900, is marked with a D on 2 dates.

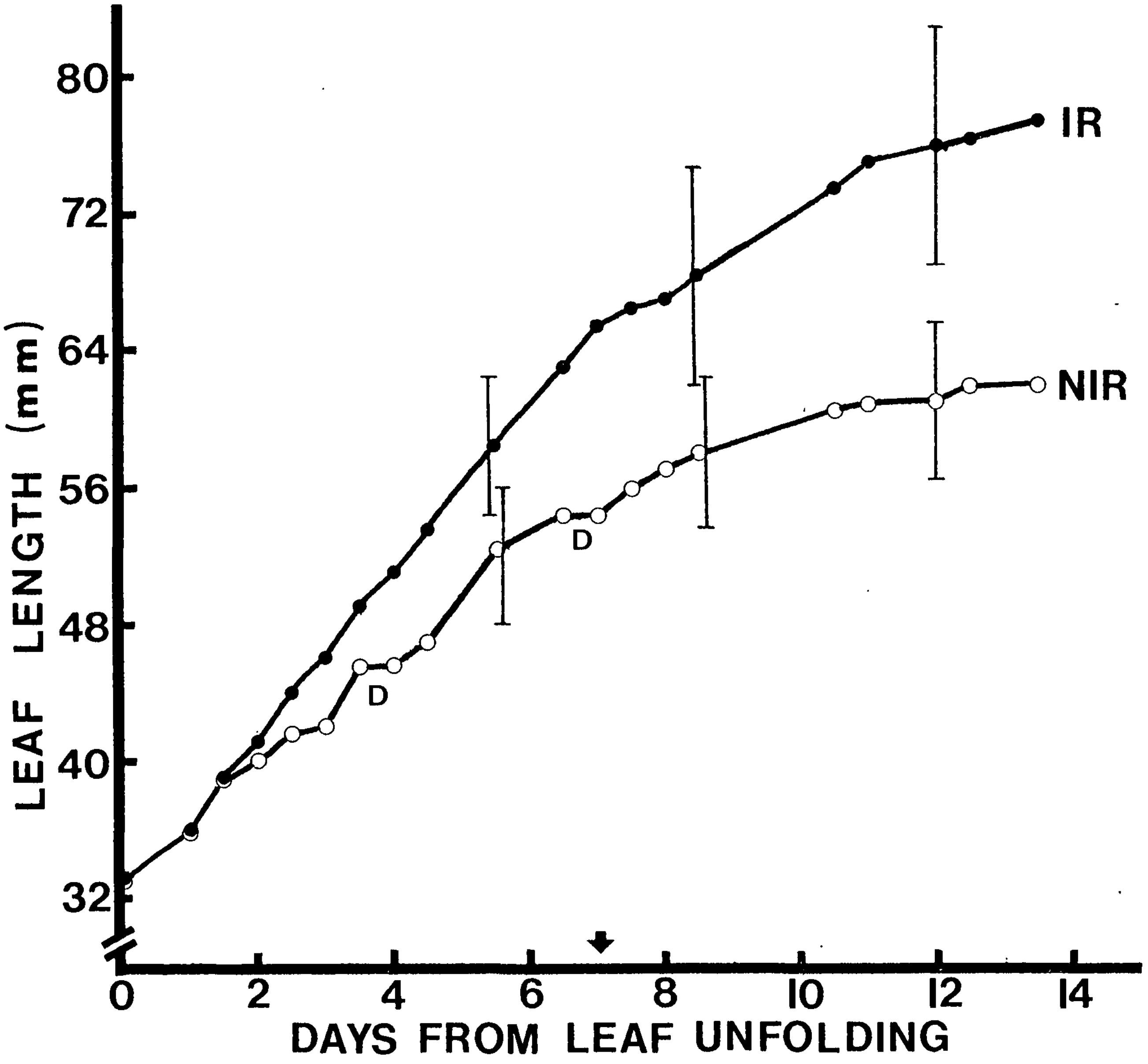

LEAF LENGTH (mm)
80
72
64
56
48
40
32
IR
NIR
D
D
0
2
4
6
8
10
12
14
DAYS FROM LEAF UNFOLDING

Figure 2. Average elongation rates of strawberry leaflets and petioles as a function of air temperature. Growth chambers were at 10, 15, 22, and 28°C. Standard errors for leaflets are marked, and are similar to those of petioles.

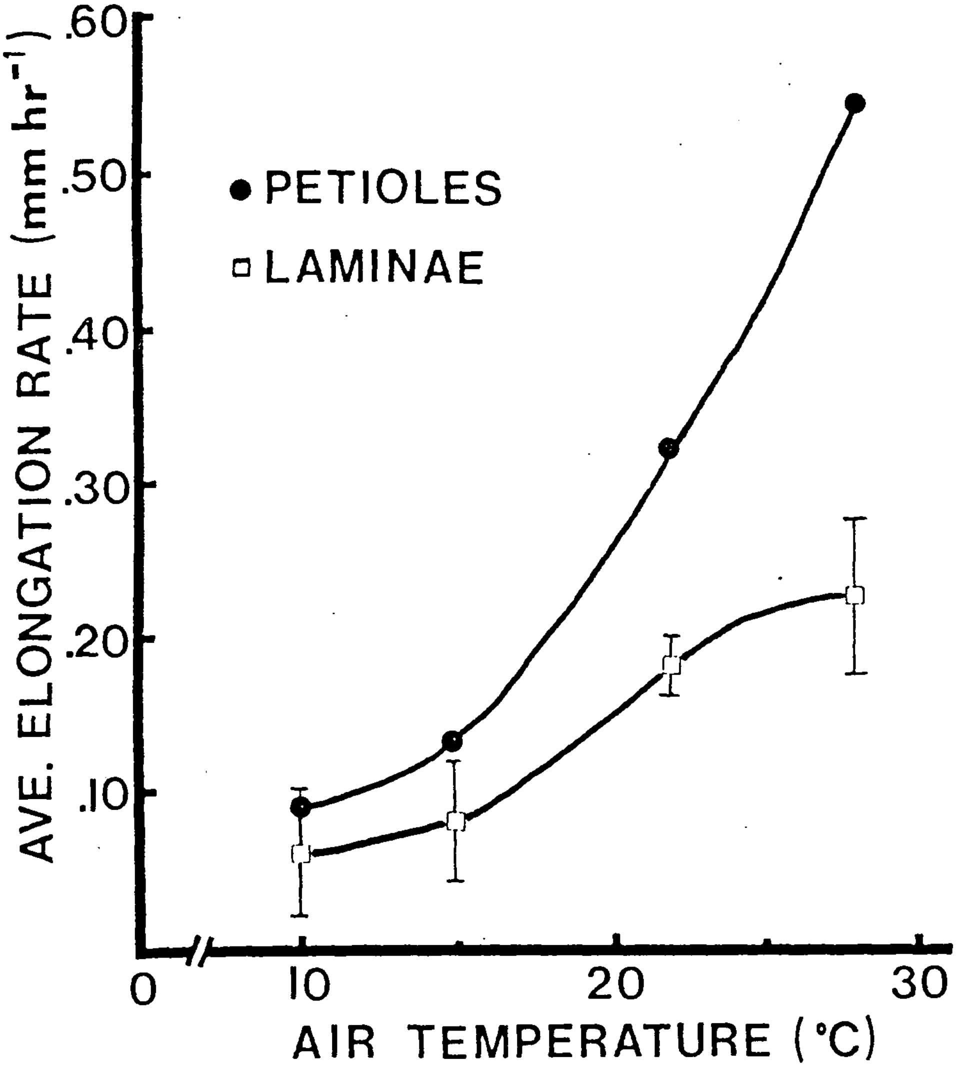
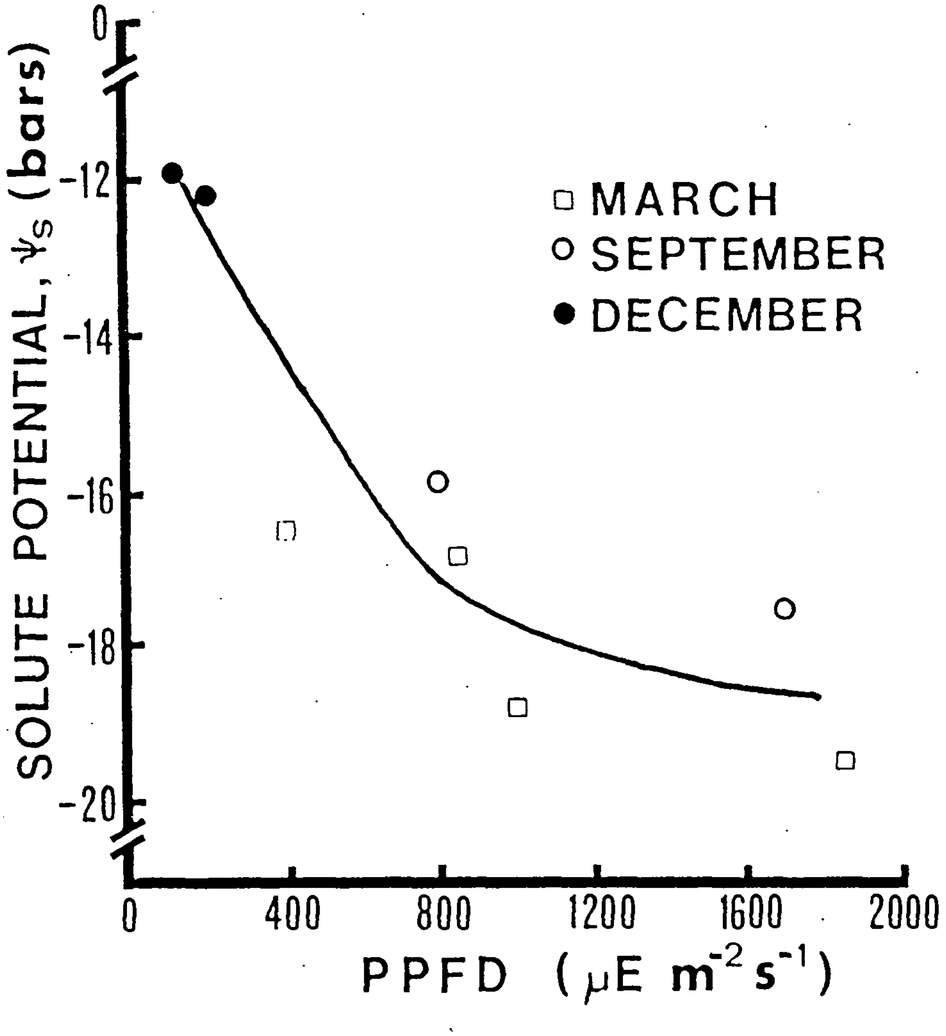

AVE. ELONGATION RATE $(mm\ hr^{-1})$
.60
.50
.40
.30
.20
.10
● PETIOLES
□ LAMINAE
0
10
20
30
AIR TEMPERATURE (°C)

Figure 3. Leaf solute potential (ψ_s) vs. photosynthetic photon flux density (PPFD) for irrigated greenhouse strawberries measured in March, September and December. All data was taken between 0930 and 1500. The 2 points at high PPFD are from plants set outside on sunny days. ψ_s for non-irrigated plants at the same light levels was 2-4 bars lower than for irrigated plants (data not shown).


0
-12
-14
-16
-18
-20
SOLUTE POTENTIAL, ψ_S (bars)
□ MARCH
○ SEPTEMBER
● DECEMBER
0
400
800
1200
1600
2000
PPFD (μE m^{-2} s^{-1})

STOMATAL BEHAVIOR AND LEAF WATER STATUS OF STRAWBERRY IN DIFFERENT GROWTH ENVIRONMENTS

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Additional index words. Water potential, osmotic potential, turgor, osmotic adjustment, light responses, leaf conductance, *Fragaria x ananassa*

Abstract. Well irrigated (IR) and non-irrigated (NIR) strawberries (*Fragaria x ananassa* Duch. cv. Olympus) were compared in terms of leaf water potential (ψ), (turgor (ψ_p), and leaf conductance (K_ℓ) during diurnal cycles in a growth chamber, greenhouse, and 2 field studies (1977 and 1979). Irrigation was withheld for 3-5 days before measurements were made in the greenhouse and growth chamber, and for 21 days (1977) and 36 days (1979) in the field. In the field minimum midday leaf ψ was usually near -15 bars in both IR and NIR plants. On clear days, such as the 1977 date, ψ and ψ_p were not greatly affected by irrigation, except that ψ in IR plants dropped more slowly in early morning and recovered faster near sunset. On the 1979 date midday ψ was higher in IR than NIR plants due to lower solar radiation, but ψ_p was very similar in the 2 treatments during most of the day. K_ℓ rates in NIR plants were half those in IR plants throughout the day, and diurnal patterns of K_ℓ were similar in 1977 and 1979 despite the differences in water status. The lower K_ℓ presumably reduced transpiration in NIR plants and may

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[1] The generous equipment loans by L. H. Fuchigami and L. Boersma are gratefully acknowledged.

explain why midday ψ was not lower than that in IR plants in 1977. Plants grown in indoor environments differed from field plants in at least 3 respects. Osmotic adjustment (solute accumulation in response to dehydration) was greatly reduced at light flux densities below 500-800 μE $m^{-2}s^{-1}$. Secondly, ψ and ψ_p of NIR plants dropped below those of IR plants as soil dried, probably due to the small pot volume. Lastly, K_ℓ at a given ψ was lower in the growth chamber than in the field, perhaps due to a direct effect of low light on stomata. A threshold ψ at which strawberry K_ℓ drops sharply (indicating stomatal closure) was not observed. The existence of such thresholds in other crops is questionable if their occurrence was inferred from leaf resistance (R_ℓ) rather than K_ℓ data.

Introduction

The rate of leaf expansion may be a sensitive indicator of water deficit in strawberry (20), yet leaf area can be reduced somewhat without greatly hindering fruit production (19). Stomatal behavior is an aspect of leaf physiology which may be more central in determining dry matter accumulation and perhaps fruit yield in response to drought. One mechanism to avoid desiccation is the control of transpiration by stomatal closure in response to low soil moisture or high evaporative demand. Leaf water status and light are 2 influences on stomatal aperature which have received considerable attention. Direct effects of humidity have also been observed in some species (5, 15, 17, 21). The greatest changes in guard cell turgor and stomatal aperature during daylight are generally attributed to changes in leaf water status. However, it is likely that there are simultaneous responses to or interactions with other factors. Interpretation of environmental effects would be much easier if the mechanism(s) of stomatal movement were known; however, they have only been partially elucidated (18).

An early report (8) on strawberry stomatal responses, using microscopic observations, noted that in drought conditions stomata were visibly open for only a brief period in the early morning. In some crops transpiration is thought to decrease appreciably with small reductions in stomatal aperature below the minimum opening which can be resolved by light microscope (22). The visual study of strawberry, therefore, may not provide an accurate picture of transpiration control throughout the day, as is possible from leaf conductance data. We have measured diurnal K_ℓ and addressed the question of how K_ℓ

is related to leaf water status and light. An additional question, which has been studied by Davies (12), is whether or not these relationships are consistent in different growth environments.

Materials and Methods

'Olympus' strawberry plants weighing 9-18 g with roots trimmed to 10 cm were established in 3-liter pots in a growth chamber and a greenhouse, as well as in the field. The container media was a 3:1 mix of silty clay loam soil and peat, fertilized as needed with soluble 30-4-8 NPK. In the greenhouse sodium vapor lights provided a 15 hr photoperiod, which promotes vegetative growth and prevents floral initiation. Photosynthetic photon flux density (PPFD) at plant height was moderately low, 210-280 μE m^{-2} s^{-1} in the growth chamber, using a mix of fluorescent and incandescent light. The midday PPFD in the greenhouse ranged from 120-400 μE m^{-2} s^{-1} during the winter and 250-1400 μE m^{-2} s^{-1} during the spring and fall. The growth chamber temperature was 18°C, while the greenhouse was 18° at night and 22-32° in the day. Old leaves were removed so that plants had a uniform canopy of 7-10 fully expanded leaves and several younger ones at the start of each experimental period. Measurements were made on leaves which had been fully expanded for approximately 1 week. Irrigation was withheld from half of the greenhouse and growth chamber plants for 3-5 days prior to the start of measurements, depending on the evaporative demand. For all experiments, data was taken on at least 4 well irrigated (IR) and 4 non-irrigated (NIR) plants at 4-6 sampling times per 24 hr. In most studies leaf ψ, K_ℓ and solute potential (ψ_s) were measured concurrently.

The field studies were on first year plantings on a fertile sandy loam soil, using drip irrigation and raised beds (19). The dates of the experimental periods, along with light, temperature, and irrigation data are listed in Table 1.

The concurrent measurement of ψ and ψ_s allows turgor potential (ψ_p) to be determined from the equation: $\psi = \psi_p + \psi_s + \psi_m$. The matric potential ($\psi_m$) was assumed to be near zero for the degree of tissue hydration involved (4). Values were expressed as bars (1 bar = 10^5 Pascals).

The leaf conductance was measured with a ventilated diffusion porometer (25), which was calibrated using a drilled plate of known theoretical conductance (14). Drift of the LiCl sensor was minimized by frequent replacement of the silica gel dessicant. Strawberry leaves are reported to have stomata on the lower surface only (9), which we verified for 'Olympus' using silicon rubber imprints. K_ℓ (which is primarily a measure of stomatal conductance) was therefore calculated from measurements on the abaxial leaf surfaces. From 1-3 of the most fully illuminated leaves on each plant were used for K_ℓ measurements throughout the diurnal cycle to reduce variability. Horizontal positioning of leaves with wire stakes also increased uniformity.

Leaf Ψ was estimated with a pressure chamber (26) and Ψ_s was estimated with a dewpoint hygrometer (6), as previously described (20).

Results and Discussion

On clear midsummer days, such as on the 1977 date, leaf Ψ in NIR plants was only lower than in IR plants (more stressed) in the early morning and late afternoon (Fig. 1C vs. 1D). There was no treatment difference in Ψ_p (data not shown). On the 1979 date evaporative demand was lower as a result of morning dew, midday clouds, and lower light levels (since it was later in the season) (Table 1). In these conditions Ψ was somewhat higher in IR than in NIR plants (Table 2, Fig. 1), however Ψ_p was again similar in the 2 treatments, except during a bried period midday (Table 2). The minimum Ψ values for NIR plants were near -15 bars in 1977, 1979 (Fig. 1D), and on other dates not reported. Minimum Ψ was usually similar in the 2 irrigation treatments, as on the 1977 date, while in 1979 the midday Ψ was higher in IR plants, probably because of their greater ability to maintain leaf hydration when evaporative demand was reduced by cloudiness. In both years Ψ of IR plants recovered more quickly at dusk than that of NIR plants (Fig. 1C, 1D), despite the fact that stomata were determined by K_ℓ measurements to be more completely closed on NIR plants. The lack of difference in midday Ψ due to irrigation can be accounted for in part by the reduced K_ℓ (stomata less open) in NIR plants at all times (Fig. 1A and 1B). Transpiration was presumably reduced enough to compensate for the lower supply of water available to the leaves of NIR plants. All plants had maximum K_ℓ rates in mid-morning, although the stomata of NIR plants apparently opened more slowly. This latter response may be due to an interaction between water status and the response to light. Darrow and Dewey (8) found that 80% of the stomata of irrigated strawberries were visibly open at 0900, only 25% at 1200, 50% at 1500 and all were closed at 1700 (2.5 hr before sunset). Under drought conditions they observed that stomata opened more slowly and the most drought resistant cultivar had a maximum of 20% of its stomata open at 0900, compared to 70-80% for other cultivars. Drought caused the stomata of all cultivars to appear closed by 1100. The K_ℓ results in Fig. 1B for NIR 'Olympus' reinforce this earlier work, since a conductance of 0.15 cm s^{-1}, which was reached by 1330, corresponded to stomata which appeared closed on silicon rubber imprints. The K_ℓ rates for both IR (0.22 cm s^{-1}) and NIR (0.07 cm s^{-1}) plants in 1979 at 1400 (Fig. 1A, 1B) may have been lower than is typical since the rapid decline in PPFD from 1450 to 600 μE $m^{-2}s^{-1}$, due to cloudiness, could have accentuated stomatal closure. The K_ℓ of IR plants at 1400 in 1979 represents a 72% decline from the morning maximum, compared to only a 30% drop by midday in IR plants in 1977. Leaf Ψ was much lower in 1977, so that the greater closure in 1979 was not due to greater water stress. Stomatal closure in late afternoon is probably also a response to decreasing light, but it may become established as a daily rhythm in strawberry since in a growth chamber study stomata started to close 2 hr before lights went off and opening occurred before the lights went on in the morning.

The diurnal course of leaf turgor was determined in the greenhouse and in 1 of the field studies reported here. To aid in interpretation of the K_ℓ and Ψ responses, Ψ_s data and the calculated Ψ_p

values are provided for the 1979 field experiment (Table 2) and 1 greenhouse study (Table 3, which also includes K_ℓ rates).

There has been much research on a wide range of crop species to determine if a relationship exists between leaf Ψ or Ψ_p and K_ℓ. Since K_ℓ is a major determinant of the rate of drop in Ψ, it is possible that the Ψ level can be self-regulated to a degree by exerting feedback control on K_ℓ. To show the K_ℓ vs Ψ relationship for strawberry without the effects of light, the measurements between 0800 and 1400 for 1 growth chamber and 2 field studies were plotted together (Fig. 2). The field data is for IR plants only. In both environments K_ℓ rates dropped gradually as Ψ decreased, and in the growth chamber stomata were essentially closed when Ψ was -15 bars (K_ℓ < 10% of maximum). Field observations of K_ℓ at high Ψ are lacking since dew was often present and also because Ψ dropped considerably by the time stomata were fully open in the morning. Stomatal closure in the growth chamber occurred over a wide range of leaf Ψ with no sharp decline in K_ℓ at a single value of Ψ.

In NIR plants K_ℓ was reduced from 0.31 to 0.06 cm s^{-1} when Ψ decreased from -5 to -15 bars. This reduction was less than the difference between the K_ℓ of IR plants and the maximum value in NIR plants, although Ψ differed by only 2 bars (-3.5 vs. -5.5) (Fig. 2). The assumption that continuity in the K_ℓ vs Ψ relationship exists between IR and NIR plants (Fig. 2, broken line) is open to question, since K_ℓ at a given Ψ in the field was consistently lower in NIR than in IR plants. This treatment difference in the K_ℓ vs. Ψ relationship could not be precisely defined since K_ℓ data from NIR plants appeared to result from a mixture of responses to both water status and light level, and are therefore omitted from Fig. 2. (The water status-light interaction is discussed in further detail below). Since K_ℓ at a given Ψ was lower in NIR than in IR plants it appears that stomata were responding to a guard cell water deficit which was not detected in terms of bulk leaf Ψ or Ψ_p. For example, the stress may involve the supply of water through the epidermis, which is considered by some workers to regulate stomatal aperture independently of bulk Ψ_p (17).

For several species, a threshold value or narrow range of Ψ or Ψ_p has been reported to correspond to stomatal closure, as shown by a rapid increase in diffusion resistance (R_ℓ) (14, 23). The concept of a threshold Ψ value has been widely used in interpreting studies on the role of abscisic acid (ABA) in stomatal control (2, 10, 27). Measured variation in the threshold Ψ has been used as an indicator of the effect of growth environment on the response of stomata to water deficit (2, 7). The choice of R_ℓ rather than its reciprocal, K_ℓ, may have unforseen consequences. The mathematical nature of a reciprocal transformation includes the possibility of converting a linear function into a quadratic one. If the inflection point in the quadratic is to be given physiological significance, then there must also be a physiological basis for choosing the quadratic function. However, transpiration is usually found to be a linear function of K_ℓ (24) and consequently cannot be as simply related to its reciprocal, R_ℓ. Since a rapid increase in R_ℓ at the inflection point does not correspond to an equally rapid decrease in transpiration, the Ψ value at the inflection should not be considered a threshold value for stomatal closure. The choice of R_ℓ rather than K_ℓ as the measure of stomatal behavior in many earlier studies caused the data to be transformed before it was examined. The literature reports of the K_ℓ vs Ψ relationship (2, 7, 10) and the results for strawberries (Fig. 2) all fail to show a threshold Ψ at which K_ℓ drops abruptly. The concept of a threshold Ψ has probably remained attractive because it fits the notion that a trigger mechanism exists for the synthesis and release of ABA from chloroplasts (18). While ABA modulation of stomata no doubt occurs, it may exert its effect over a wider range of Ψ than was initially thought. ABA-induced closure may also be preceded by a decrease in K_ℓ in response to other factors (17, 18, 21). Apparent reductions in threshold Ψ due to stress pre-conditioning or growth environemnt (2, 7) might be more meaningfully described in terms of changes in the slope of the K_ℓ vs Ψ relation. A lower slope for the K_ℓ response to decreasing Ψ means that stomata are closing more slowly over a wider range of Ψ, rather than at a lower apparent threshold Ψ (but the same rate) as previously suggested. This is in accord with the observation that sorghum stomata closed over a 10 bar range when stress developed at a rate representative of field conditions (13).

Stomatal responses to water deficit and low or decreasing light levels apparently interact in strawberry. The very low midday K_ℓ of both IR and NIR plants in the field in 1979 was ascribed above to the rapid decline in PPFD. This decline should have affected IR and NIR plants equally, yet the midday K_ℓ of IR plants was 3 times greater than that of NIR plants and was reduced less between 1100 and 1400 hr

(Fig. 1) on a percentage basis also (59% vs 80%). These observations, along with the slower stomatal opening in NIR strawberries after sunrise, are evidence for an interaction between the stomatal responses to light and water status. Such interaction also appeared in the stomatal behavior of eggplant (3). The more common view regarding light effects is that abaxial stomata are quite insensitive to changes in PPFD within the normal daytime range (15). The question of species variation in this regard should be more fully explored. A mechanism in which water deficit sensitizes the stomatal closing response to low light would efficiently postpone water stress by reducing transpiration at times when open stomata are of little benefit. Another example of this type of interaction was reported by Kaufmann (16), in which the size of the leaf-to-air absolute humidity difference required to cause stomatal closure was lower in the shade than in the sun.

The question of what influence growth environment has on K_ℓ and/or its components is an important one, since most data on crop species has been obtained from growth chamber and greenhouse-grown plants. Some effects of light intensity on K_ℓ in the field were discussed above. Since PPFD was much lower in the controlled environments, the consistently lower K_ℓ at each level of Ψ in the growth chamber vs. the field (Fig. 2) is perhaps an effect of the difference in light. This is supported by the observation that the 2 treatment means for K_ℓ in the field when midday light was low (Fig. 2, stars) fell very close to the growth chamber curve. An alternative explanation is that morphological differences, such as the frequency of stomata, were present in plants grown in the different environments.

Osmotic adjustment, the maintenance of Ψ_p in response to dehydration, was influenced by the light environment (20), suggesting a possible indirect effect of light on stomata if Ψ_p and K_ℓ are closely related. The data indicated that accumulation of solutes, which are often carbohydrates in crops which osmotically adjust (1), was reduced in strawberries by the light levels below 500-800 $\mu E\ m^{-2}\ s^{-1}$ in the growth chamber and winter greenhouse experiments (20). The accumulation of solutes lowers Ψ_s, inducing water movement into cells so that Ψ_p is higher at a given Ψ. The average difference in Ψ_s between field treatments was about 3 bars (lower in NIR than IR plants, see Table 2), and part of this was a simple concentration effect due to greater dehydration in NIR plants. The loss of water can't sustain turgor unless there is an increase in cell wall elasticity (11), which has not been widely observed. However, this relatively modest degree of osmotic adjustment in field-grown strawberries was sufficient to prevent irrigation treatment differences in Ψ_p during most of the times when Ψ was higher in IR than in NIR plants (Table 2). Yet K_ℓ of IR plants was double that of NIR plants throughout the day (Fig. 1A vs. 1B). Clearly, a unique relationship between Ψ_p and K_ℓ was lacking. This was also observed by Turner (24) in maize, prompting him to part with his earlier suggestion that Ψ_p and K_ℓ are closely linked (23). Since Ψ_p maintenance did not prevent reduced K_ℓ in NIR strawberries, it appears that the indirect effect of low light on K_ℓ via solute levels may be minor in comparison with the direct effect hypothesized earlier. It is noteworthy, however, that the capability for osmotic adjustment would have been overlooked had data only been taken on indoor plants (Table 4).

Another difference in strawberry behavior between growth environments was that while diurnal Ψ of IR and NIR plants was quite similar on sunny days in the field, Ψ was lower in NIR plants in the greenhouse. The separation between treatment means increased during the course of a drying cycle (Fig. 3). This was apparently due to the combined effects of 2 environmental factors. The lower level of solar radiation in the greenhouse reduced the midday drop in Ψ in the IR plants, much as it did in the field on the cloudy day in 1979 (Fig. 1C). The second factor was the small soil volume in pots, which resulted in greater depletion of soil water and a very low minimum Ψ in NIR plants in the greenhouse. Ψ fell to -23 bars on the third day of the drying cycle, of which only the first 2 days are presented in Fig. 3. In contrast, Ψ never dropped below -16 bars in the field even when evaporative demand was very high (Table 1), and overnight recovery of Ψ and Ψ_p always occurred.

Minimum daytime K_ℓ in NIR plants was also lower in the greenhouse (Table 3) than in the field. The primary cause was probably the more severe soil moisture deficit, although it was often not reflected in the leaf Ψ.

In conclusion, stomatal response to soil water deficit was apparent in strawberry, but the relationship of K_ℓ to leaf Ψ or Ψ_p depended on the growth environment and the irrigation history (IR vs. NIR plants), and was also subject to alteration by other influences on stomata. While the different functional responses of plants to water stress are probably integrated by general metabolic factors, it is also possible that distinct facets of water stress exist. Strawberry stomata may respond to some facet which is not reflected in bulk leaf Ψ or Ψ_p. Until the internal factors that relate water status to stomatal function are defined, it may be more useful to directly utilize K_ℓ measurements as an index of stress in strawberries rather than measure water potential or turgor and attempt to interpret their significance. Used together with measurements of leaf elongation rate (20), it may be feasible to establish a physiological basis for strawberry irrigation requirements without having to wait for the many complex water-growth relationships to be elucidated.

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Table 1. Environmental data during the experimental periods for 2 field plantings of 'Olympus' strawberry. Planting dates were in May of 1977 and 1979.

Date of sampling	August 10, 1977	August 25, 1979
Maximum temperature (°C)	39.5	29.5
Minimum temperature (°C)	17.8	12.2
Midday average PPFD ($\mu E\ m^{-2}\ s^{-1}$)	2000	1100
Wind run (km day^{-1})	88	48
Class A pan evaporation (cm day^{-1})	1.42	0.41
Cloud condition	clear	clouds 1200-1500
Duration of irrigation treatments (days)	21	36

Table 2. Diurnal solute potential (Ψ_s) and turgor potential (Ψ_p) of leaves from irrigated (IR) and non-irrigated (NIR) strawberries in the field on August 25, 1979. Environmental data is in Table 1.

Time	Treatment	Ψ (bars)	Ψ_s (bars)	Ψ_p (bars)
0500	IR	- 1.1 ± 0.3	-15.3 ± 1.3[z]	14.2 ± 1.1
	NIR	- 4.3 ± 0.9	-18.8 ± 1.5	14.5 ± 1.2
0800	IR	- 1.3 ± 0.3	-16.4 ± 0.7	15.1 ± 0.6
	NIR	- 5.0 ± 1.3	-19.7 ± 2.0	14.7 ± 2.2
1100	IR	-11.1 ± 0.9	-18.7 ± 1.1	7.6 ± 2.0
	NIR	-14.8 ± 1.0	-22.4 ± 1.2	7.6 ± 1.1
1400	IR	-10.0 ± 1.1	-20.6 ± 1.4	10.6 ± 2.1
	NIR	-15.3 ± 0.9	-21.6 ± 1.2	6.3 ± 1.8
1700	IR	-10.6 ± 0.9	-19.5 ± 0.4	8.9 ± 0.7
	NIR	-15.6 ± 0.9	-22.4 ± 0.7	6.8 ± 1.2
2000	IR	- 2.3 ± 0.3	-17.4 ± 1.0	15.1 ± 0.7
	NIR	- 7.5 ± 1.2	-22.4 ± 1.6	14.9 ± 2.7

[z] ±SE

Table 3. Diurnal solute potential (Ψ_s), turgor (Ψ_p) and leaf conductance (K_ℓ) of leaves from irrigated (IR) and non-irrigated (NIR) strawberries in a greenhouse, starting March 22, 1979. The photoperiod was from 0700 to 2100.

Time	Treatment	Ψ_s (bars)	Ψ_p (bars)	K_ℓ (cm s^{-1})
1430	IR	--	--	.29 ± .12
	NIR	--	--	.20 ± .10
1700	IR	-18.8 ± 1.4[z]	12.1 ± 0.7	.20 ± .03
	NIR	-18.8 ± 2.3	8.3 ± 1.4	.10 ± .02
2000	IR	-17.0 ± 0.8	14.8 ± 1.0	.05 ± .02
	NIR	-17.2 ± 1.0	10.4 ± 1.1	.01 ± .008
0500	IR	-16.1 ± 0.7	14.6 ± 0.7	.04 ± .02
	NIR	-16.1 ± 0.5	10.7 ± 1.0	.01 ± .004
0930	IR	-16.8 ± 2.0	9.2 ± 1.4	.77 ± .15
	NIR	-18.2 ± 1.3	3.7 ± 1.4	.04 ± .03
1300	IR	-18.8 ± 0.9	8.4 ± 1.0	.20 ± 0.5
	NIR	-19.3 ± 2.4	4.0 ± 2.7	.01 ± .001

[z] ±SE

Figure 1. Diurnal leaf conductance (K_ℓ) and leaf water potential (Ψ) in irrigated (IR) and non-irrigated (NIR) strawberries in 2 first-year plantings. A) K_ℓ in IR plants; B) K_ℓ in NIR plants; C) Ψ in IR plants; D) Ψ in NIR plants. Dates and weather data are listed in Table 1. K_ℓ data is plotted together for the 2 years. Morning dew prevented K_ℓ determination at 0600 in 1979. The bars represent ± SE.

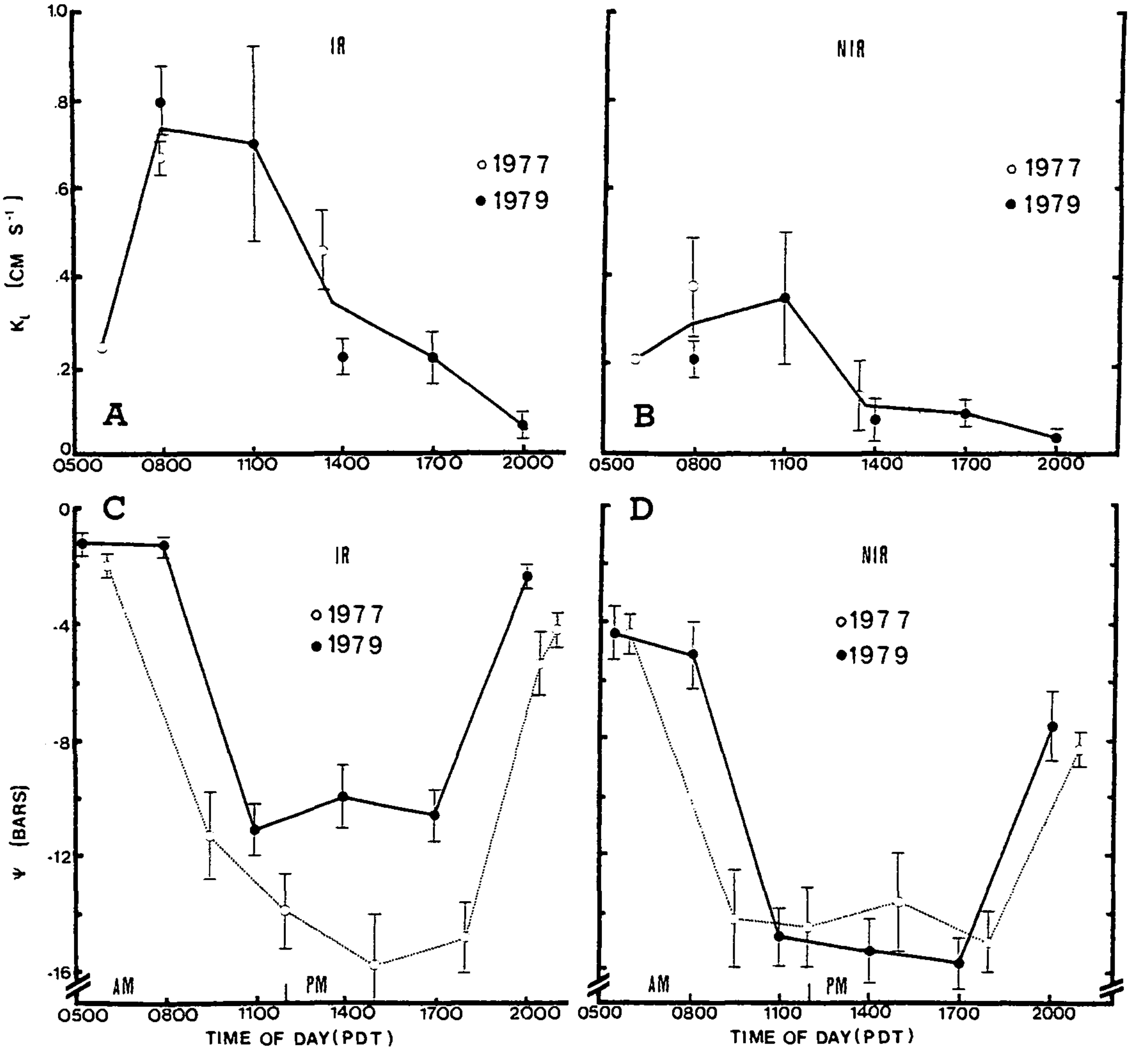

A
B
C
D
IR
NIR
○1977
●1979
K_l (CM S^{-1})
Ψ (BARS)
1.0
.8
.6
.4
.2
0
-4
-8
-12
-16
AM
PM
0500
0800
1100
1400
1700
2000
TIME OF DAY(PDT)

Figure 2. Leaf conductance (K_ℓ) vs. leaf water potential (Ψ) for strawberries in a growth chamber or in the field. All observations were made between 0800 and 1400. Growth chamber plants were either irrigated (IR) or non-irrigated (NIR). Field data is from IR plants on days in 1977 and 1979. The stars represent treatment means in the field in 1979 when midday light was low (IR = open star, NIR = solid star; see text for discussion). The dashed line approximates the K_ℓ vs. Ψ relationship in NIR growth chamber plants during the first 4 days of treatments. The bars represent ± SE.

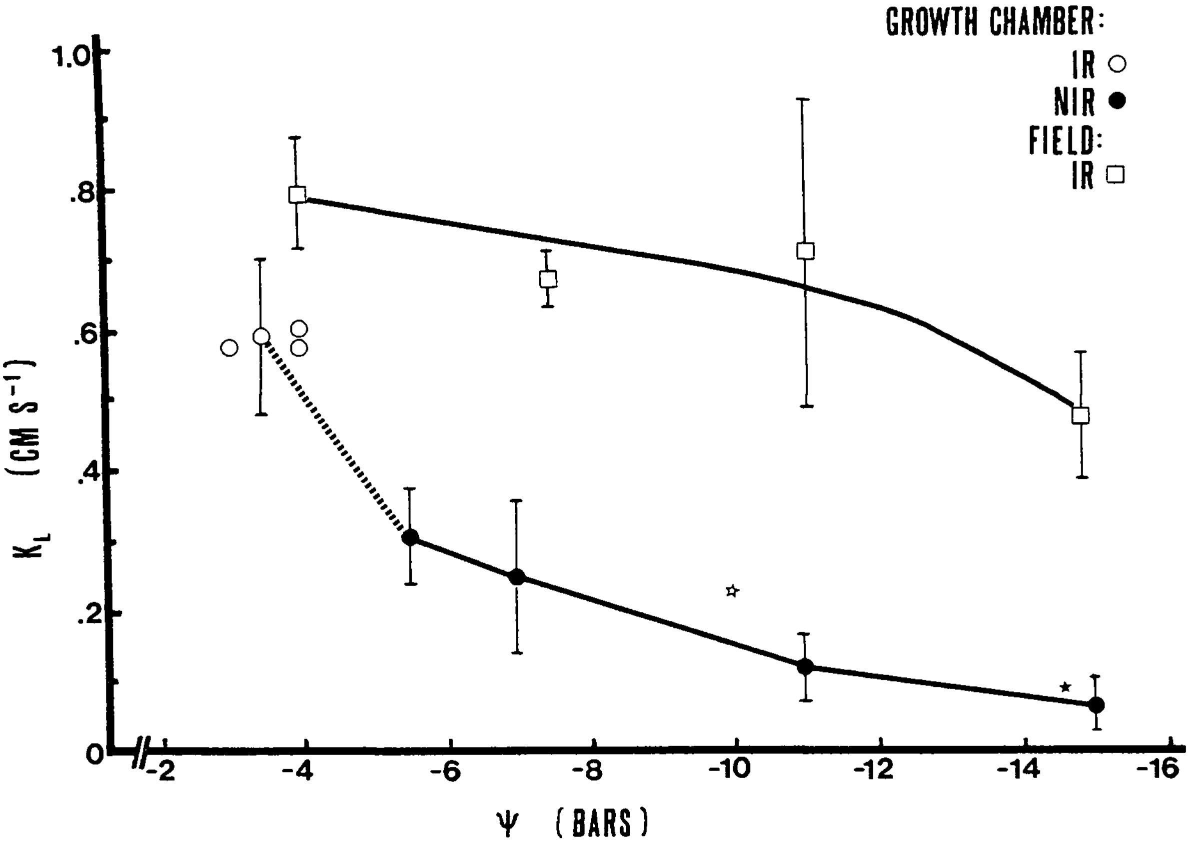
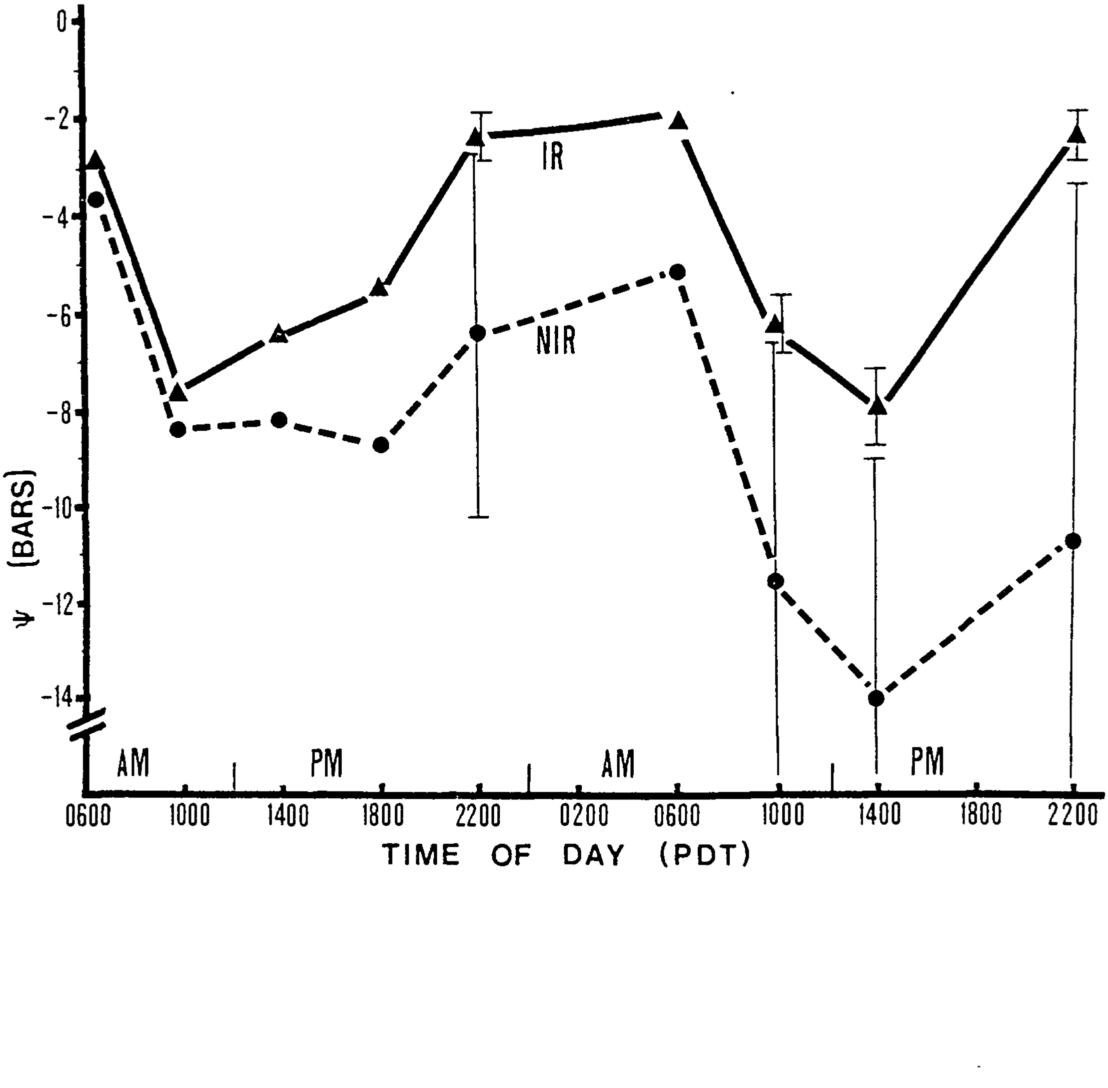

GROWTH CHAMBER:
IR ○
NIR ●
FIELD:
IR □
K_L (CM S^{-1})
1.0
.8
.6
.4
.2
0
-2
-4
-6
-8
-10
-12
-14
-16
Ψ (BARS)

Figure 3. Diurnal leaf water potential (Ψ) of irrigated (IR) and non-irrigated (NIR) strawberries in a greenhouse on May 6, 1978. The bars represent ± SE.


0
-2
-4
-6
-8
-10
-12
-14
ψ (BARS)
IR
NIR
AM
PM
AM
PM
0600
1000
1400
1800
2200
0200
0600
1000
1400
1800
2200
TIME OF DAY (PDT)

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APPENDICES

Table A-1. Weekly maximum and minimum mean soil temperatures (°C) at 10 cm depth below strawberries at low (L) and high (H) rates of irrigation, with or without polyethylene (P) mulch. Data is from the third week (July 22-28) through the tenth week after the start of treatments in the 1978 planting.

Treatment	Week Number							
	3	4	5	6	7	8	9	10
L max.	28	28	29	23	19	22	18	17
min.	21	20	22	19	17	17	16	14
LP max.	31	31	32	25	21	25	20	19
min.	23	21	23	19	18	18	17	19
H max.	28	28	28	21	18	22	18	17
min.	21	21	21	18	16	17	15	14
HP max.	30	32	32	23	19	24	19	18
min.	26	23	24	20	18	19	17	16

Table A-2. Difference in diurnal soil temperature (black polyethylene mulch minus unmulched) at 7.5 cm and 10 cm depth on days with maximum air temperatures of 30-35°C. Maximum and minimum temperatures at 7.5 cm depth with a medium (M) rate of irrigation and no mulch were 18° and 34°. Data at 10 cm is for irrigation at both low (L) and high (H) rates of irrigation.

Time of Day	Depth and Treatment		
	7.5 cm (MP vs M)[z/]	10 cm (LP vs. L)	10 cm (HP vs H)
0600	4.5°C	4.0	3.5
0800	4.0	3.5	3.5
1000	3.0	2.0	3.0
1200	2.0	1.5	3.0
1400	3.5	1.5	3.0
1600	4.5	1.0	3.0
1800	4.5	1.0	3.5
2000	4.5	1.5	3.5
2200	4.5	2.0	3.5
0000	4.5	3.0	3.5
0200	4.5	3.5	3.5
0400	4.5	4.0	3.5
24 hr. aver.	4.0	2.5	3.0

[z/] P = polyethylone mulch.

Table B-1. Effect of irrigation regime and poly mulch on the number of stolons per plant produced during the first season of two plantings. Irrigation treatments were low (L), medium (M), and high (H), with or without polyethylene (P) mulch.

Treatment	1977 Planting	1978 Planting
L	3.3	8.5
LP	6.0	11.0
M	6.2	9.3
MP	8.5	13.4
H	12.1	13.6
HP	6.8	14.5

Table B-2. Effect of two summers of differential irrigation and 26 months with or without poly mulch on the number of flowers, number of fruit, and fruit yield per plant in 1979 (1977 planting). Irrigation treatments were low (L), medium (M), and high (H), with or without poly (P) mulch. No statistical differences between treatments were detected.

Treatment	Flowers	Fruit	Fruit Yield (g/plant)
L	307	141	883
LP	281	118	770
M	333	133	874
MP	325	131	854
H	309	136	755
HP	273	139	862

Figure B-1. Effect of irrigation and poly mulch on the number of crowns per plant during the 1977 season. The irrigation regimes were low (L), medium (M), and high (H), with or without polyethylene (P) mulch (solid lines = mulched).

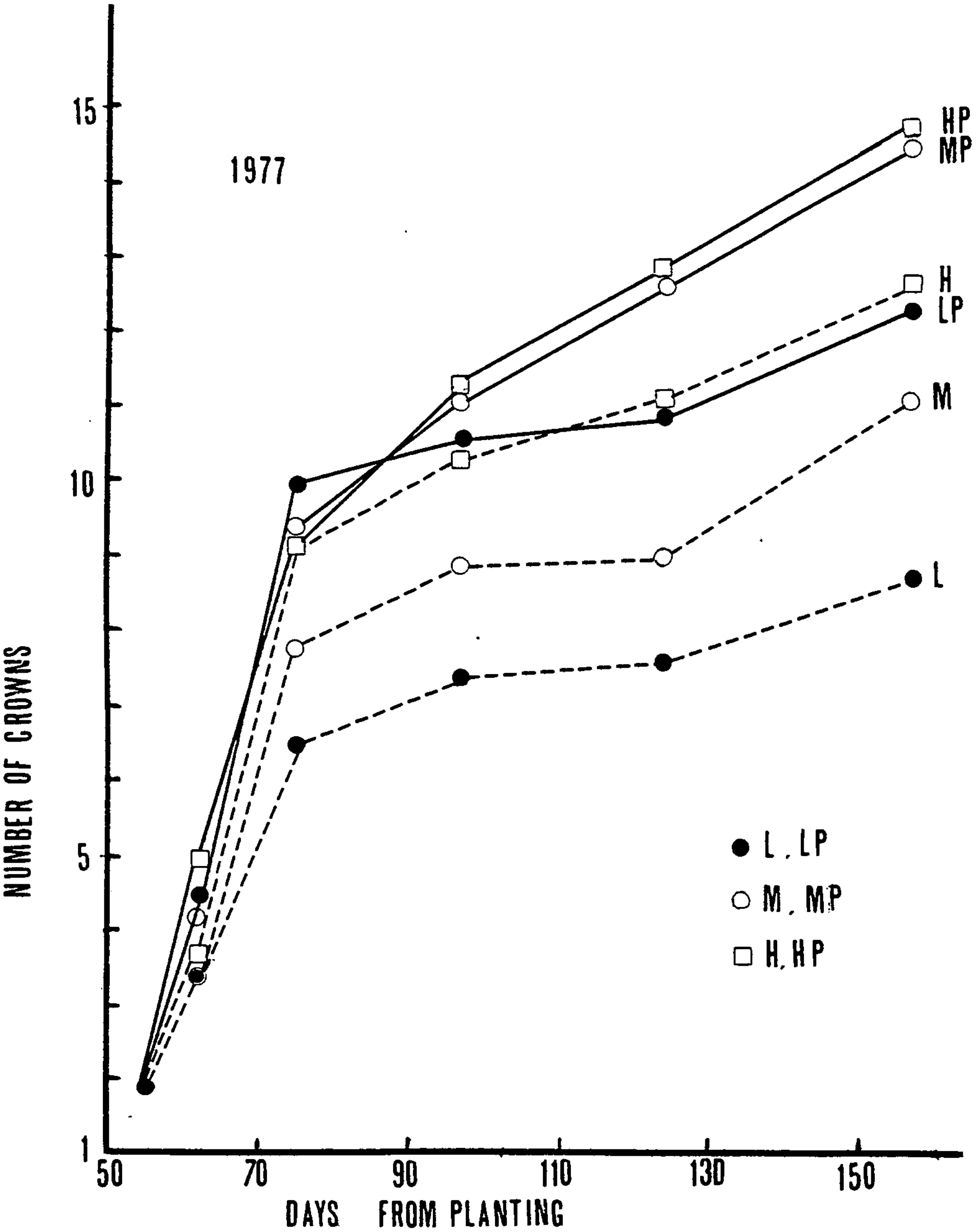

1977
NUMBER OF CROWNS
DAYS FROM PLANTING
1
5
10
15
50
70
90
110
130
150
HP
MP
H
LP
M
L
● L, LP
○ M, MP
□ H, HP

Figure B-2. Effect of irrigation and poly mulch on the number of leaves per plant during the 1977 season. The irrigation regimes were low (L), medium (M), and high (H), with or without polyethylene (P) mulch (solid lines = mulched).

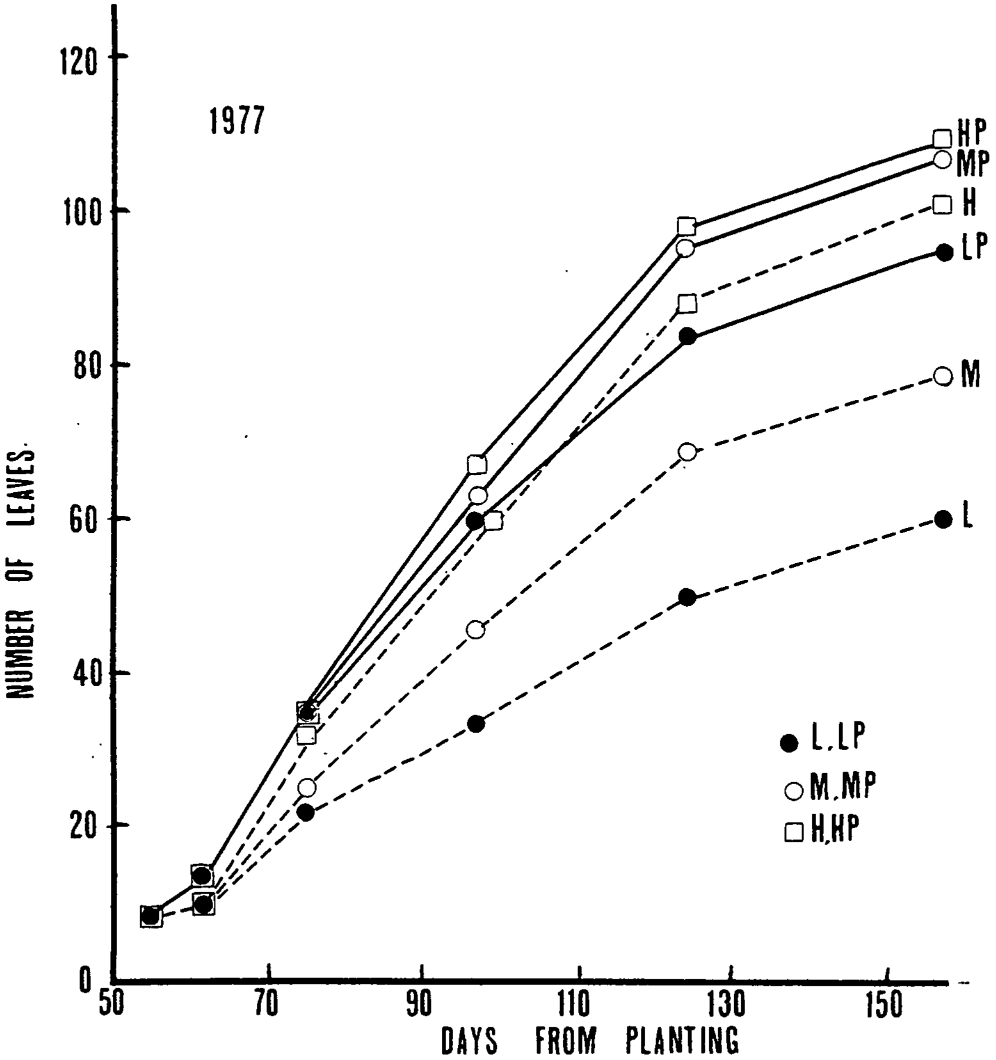

1977
NUMBER OF LEAVES
DAYS FROM PLANTING
0
20
40
60
80
100
120
50
70
90
110
130
150
HP
MP
H
LP
M
L
● L,LP
○ M,MP
□ H,HP

Figure B-3. Effect of irrigation and poly mulch on the number of crowns per plant during the 1978 season. The irrigation regimes were low (L), medium (M), and high (H), with or without polyethylene (P) mulch (solid lines = mulched).

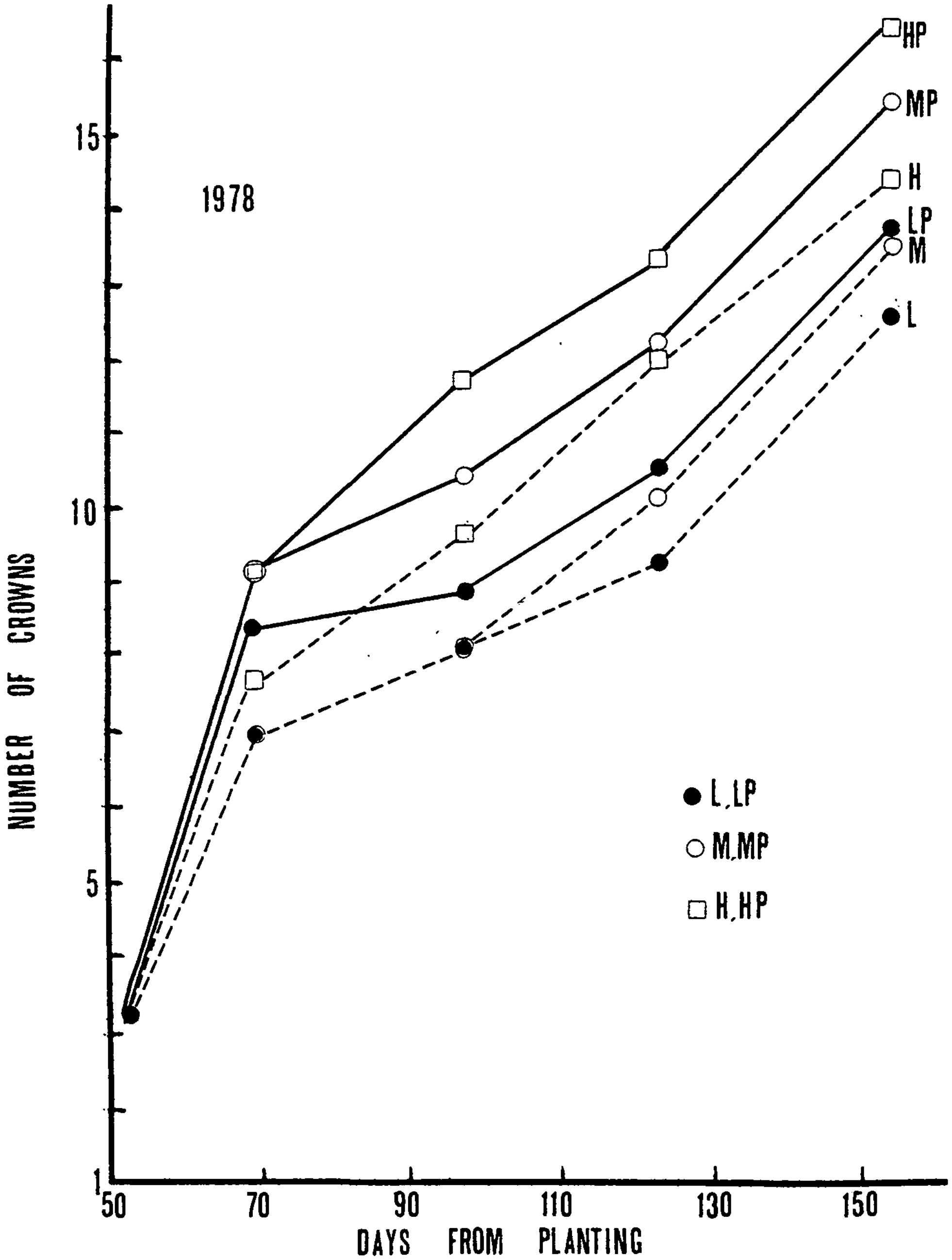

1978
NUMBER OF CROWNS
DAYS FROM PLANTING
1
5
10
15
50
70
90
110
130
150
HP
MP
H
LP
M
L
● L,LP
○ M,MP
□ H,HP

Figure B-4. Effect of irrigation and poly mulch on the number of leaves per plant during the 1978 season. The irrigation regimes were low (L), medium (M), and high (H), with or without polyethylene (P) mulch (solid lines = mulched).

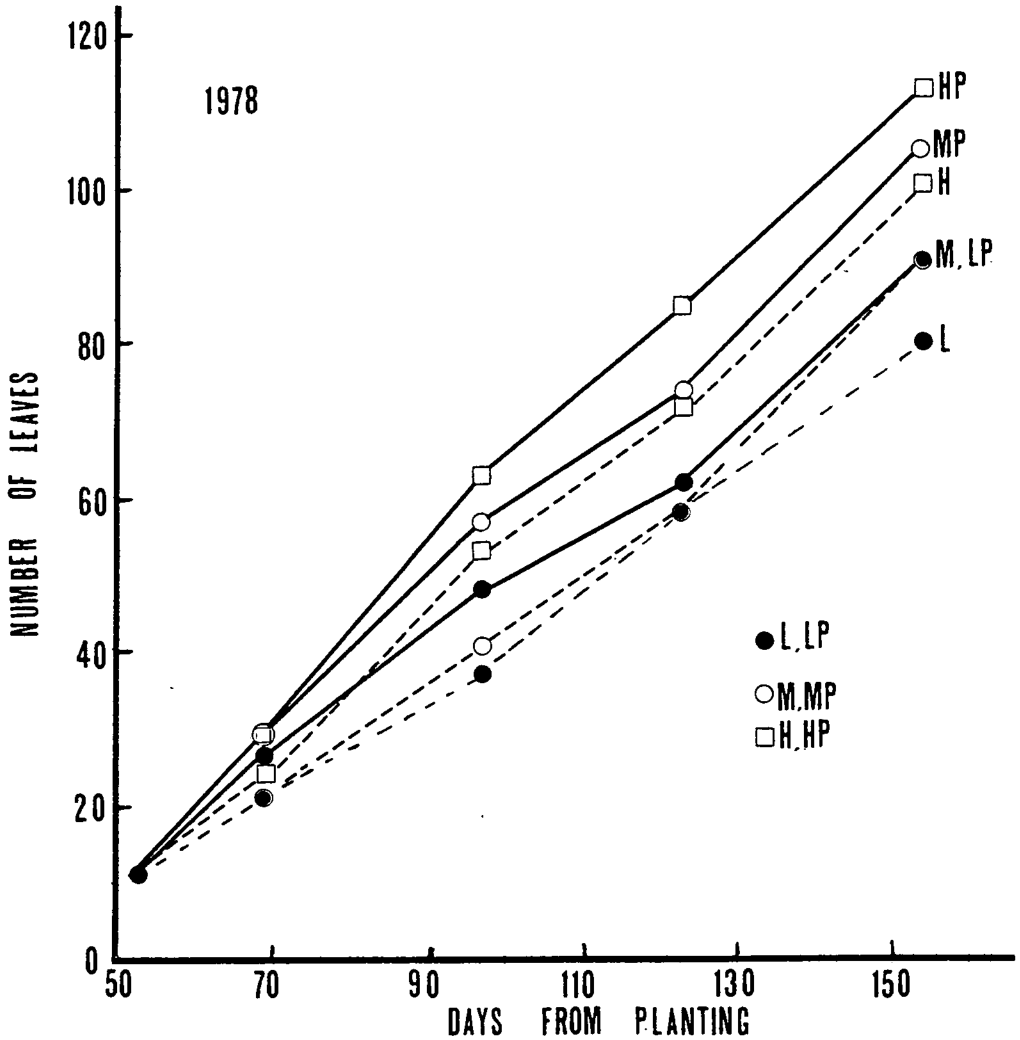

1978
NUMBER OF LEAVES
DAYS FROM PLANTING
0
20
40
60
80
100
120
50
70
90
110
130
150
HP
MP
H
M, LP
L
● L, LP
○ M, MP
□ H, HP

Figure C-1. Effect of polyethylene (P) mulch on the rate of strawberry leaflet elongation at low (L) or high (H) rates of irrigation. Measurements were started on July 28, 1978. Black bars indicate night periods.

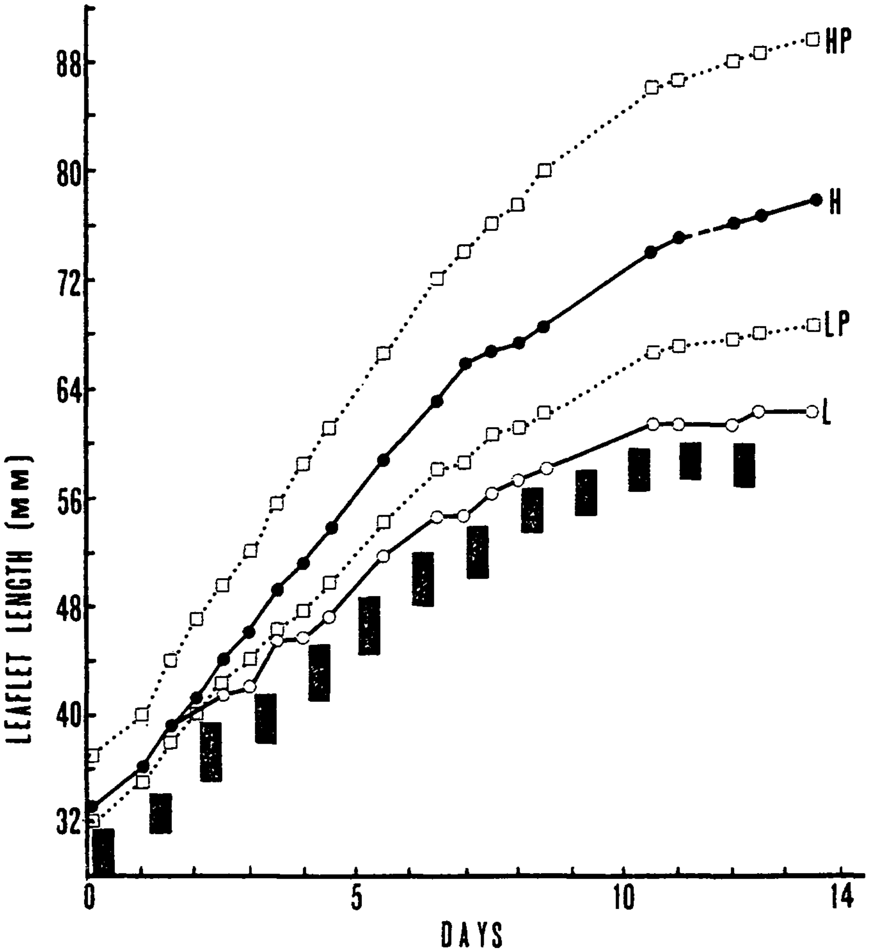

LEAFLET LENGTH (MM)
32
40
48
56
64
72
80
88
DAYS
0
5
10
14
HP
H
LP
L

Figure C-2. Effect of irrigation regime and polyethylene mulch on diurnal leaf water potential on August 11, 1977. Irrigation rates were low (L) or high (H), with or without polyethylene (P) mulch. The H treatment did not differ significantly from the HP treatment.

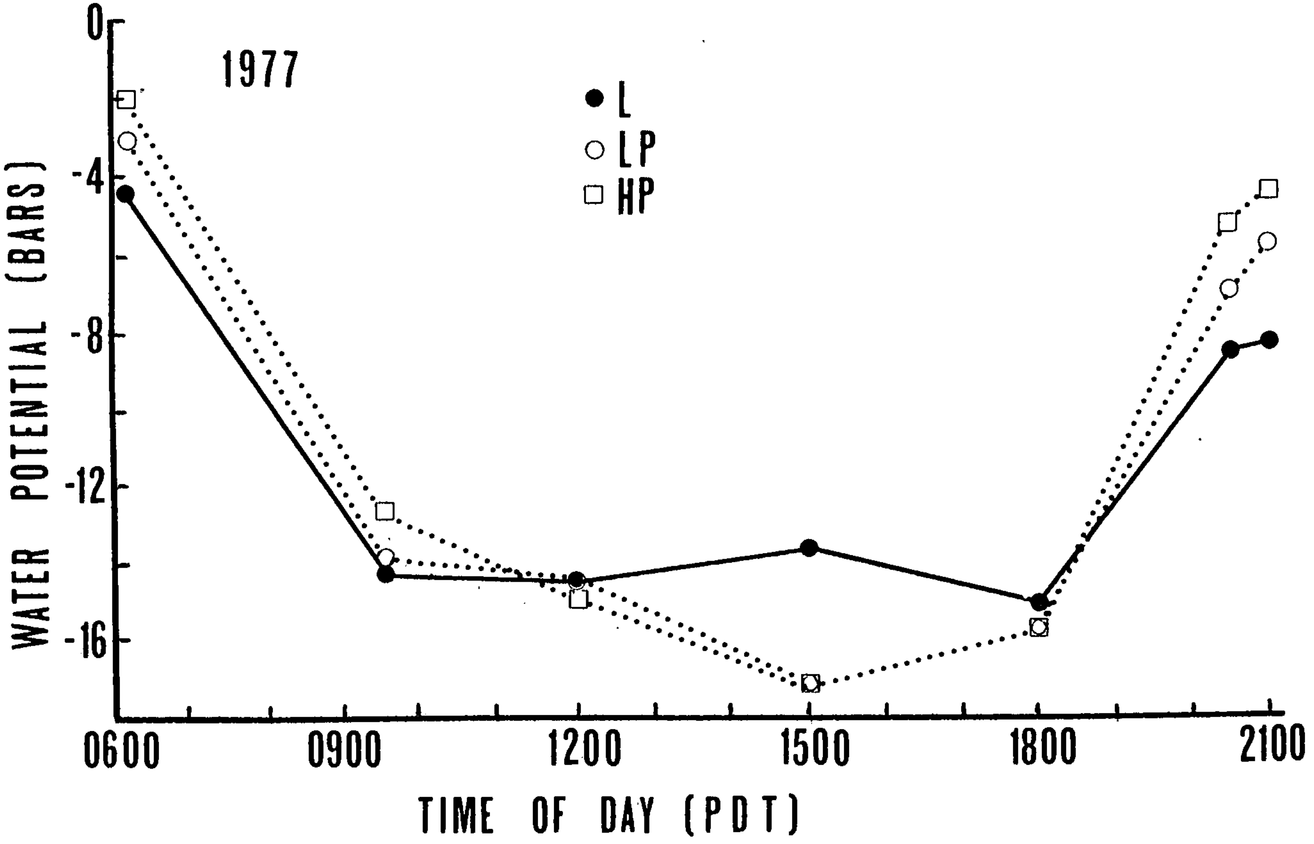
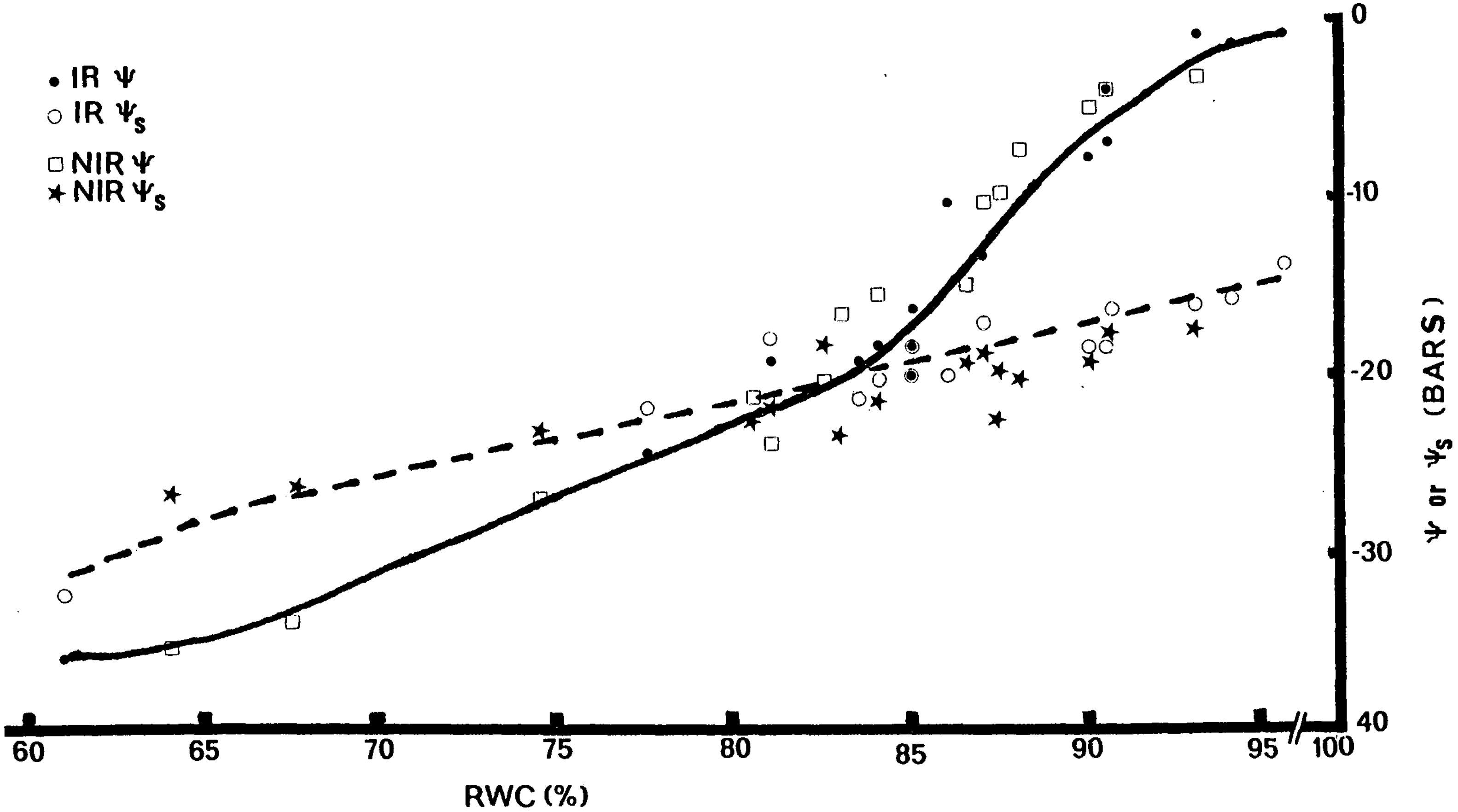
1977
● L
○ LP
□ HP
WATER POTENTIAL (BARS)
0
-4
-8
-12
-16
0600
0900
1200
1500
1800
2100
TIME OF DAY (PDT)

Figure D-1. Moisture release curve: water potential (Ψ) and solute potential (Ψ_s) vs. relative water content (RWC) in leaves of irrigated (IR) and non-irrigated (NIR) strawberries. Leaves were excised at 0700 on September 1, 1979 (NIR) and September 5, 1979 (IR). Curves were eye-fitted to the data for IR plants and indicate zero turgor (intersect) at approximately 83% RWC, compared to about 80% for NIR plants. Ψ_s in NIR plants averaged 2-3 bars lower than in IR plants in the range of positive turgor, indicating a moderately low degree of osmotic adjustment in response to drought (42 days NIR).


• IR Ψ
○ IR Ψ_s
□ NIR Ψ
★ NIR Ψ_s
0
-10
-20
-30
40
Ψ or Ψ_s (BARS)
60
65
70
75
80
85
90
95
100
RWC (%)