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The Effects of Water-stress, Rootstock, and Crop Load On Carbohydrate Partitioning and Gas Exchange of Seyval Grapevines During Year One and Year Two of Vineyard Establishment

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THE EFFECTS OF WATER-STRESS, ROOTSTOCK, AND CROP LOAD ON CARBOHYDRATE PARTITIONING AND GAS EXCHANGE OF SEYVAL GRAPEVINES DURING YEAR ONE AND YEAR TWO OF VINEYARD ESTABLISHMENT

By

Robert Michael McLean

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ABSTRACT

THE EFFECTS OF WATER-STRESS, ROOTSTOCK, AND CROP LOAD ON CARBOHYDRATE PARTITIONING AND GAS EXCHANGE OF SEYVAL GRAPEVINES DURING YEAR ONE AND YEAR TWO OF VINEYARD ESTABLISHMENT

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Berries, shoots, and fine roots of grapevines are all powerful carbohydrate sinks at some time during vine development. However during periods of soil-moisture stress, the relative strength of these sinks is not known. This experiment was conducted to evaluate interrelationships among differing crop loads and water-stress on photosynthesis, and carbohydrate partitioning for above-and below-ground tissues of Seyval grapevines grafted on three different root systems. Two-year-old grapevines grafted to different root systems were exposed to water and crop load stress to determine photosynthesis variables: net $C0_2$ assimilation (A), stomatal conductance (g_s), transpiration (E), and water use efficiency (WUE). Leaf abscisic acid (ABA) content of vines grown under different irrigation and crop load levels was investigated. Root development and depth were determined by quantifying root images from video recordings taken to depths of 80 cm at approximately two-week intervals throughout the growing season. Two-year-old own-rooted and Seyval grafted to 5BB and Seyval were grown under a rain exclusion shelter. Treatments were: 1) cropping level, either 0 or 6 clusters/vine, and 2) irrigation

level, either 10 or 2.5 liters of water/plant/week. Results indicated that g_s was affected greater than A. Fruited vines had greater g_s, E, and lower WUE and leaf dry weight (DW) compared to defruited vines. Vines grown under water-stress had lower A, g_s, E, and DLF, and higher WUE compared to vines grown under the control-irrigated level. ABA content of water-stressed leaves were greater than the leaves of control-irrigated vines. There were rootstock effects to ABA content in leaves. Total root number m^{-2}, shoot length, number of mature nodes, leaf area and DW of vines under high cropping level were reduced compared to vines growing under the low cropping level. Conditions of low soil-moisture resulted in carbohydrate partitioning in favor of the clusters at the expense of the fine roots, and carbohydrate partitioning in favor of the roots at the expense of the above-ground vegetation.

DEDICATION

This dissertation is dedicated to my wife, Amy Sakai McLean.

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Guidance Committee:

The journal-article format was adopted for this dissertation in accordance with departmental and university requirements. Each section was prepared as a self-standing manuscript so there is some duplication in the Materials and Methods portion of some sections of the dissertation. Section I was prepared as a literature review not intended for publication. Sections II, III and IV were prepared for publication in the *American Journal of Viticulture and Enology*.

INTRODUCTION

Roots play important roles in the growth and development of grapevines. Among these are: pest resistance (Howell, 1987); water (Sharp and Davies, 1979) and nutrient uptake (Atkinson, 1980); support (Winkler, 1974); cold hardiness (Miller *et al.*, 1988; Striegler and Howell, 1991); storage of carbohydrates (Richards, 1986; Rom, *et al.*, 1986); osmotic adjustment (Westgate and Boyer, 1985); shoot signals, via growth substances to control carbon allocation for growth (Feldman, 1984; Proebsting *et al.*, 1989; Zhang and Davies, 1987, 1989, 1990). Grapevines and other fruit crops are also often grafted to rootstocks so a bi-genic organism is produced with the rootstock selected for fruit quality/composition goals as well as soil related concerns such as phyloxera, nematodes and soil pH.

While there is much literature on above-ground plant functions, roots are much less studied because of obvious difficulties of observing and measuring roots *in situ*, and most of the qualitative studies have used destructive methods (Bohm, 1979; Atkinson, 1980; Upchurch and Ritchie, 1983). Since roots influence so many vine growth and fruit composition factors, a non-destructive methodology for evaluating the dynamics of root growth and turnover as related to above-ground vine activities would be very valuable.

Leaf and shoot (Smart, 1974; During and Loveys, 1982; Natali, *et al.*, 1985; Matthews *et al.*, 1987; Zobel, 1990; Proebsting *et al.*, 1989; Ranny *et al.*, 1991), rootstock (Maggioni, 1980; Pongracz, 1983; Carbonneau, 1985; Williams, and Smith, 1991; Candolfi-Vasconcelos *et al.*, 1993) and crop load (Kliewer *et al.*, 1969, 1973;

Bravdo *et al.*, 1985; Motomura, 1990) have been evaluated in response to water stress. Much less work has been done to quantify root and rootstock behavior (Maggioni, 1980) and root distribution (Williams and Smith, 1991), and the same is true regarding *in situ* root function and development (Glen and Welker, 1992), root growth dynamics (Upchurch and Ritchie, 1983; Feldman, 1984). Quantification of roots morphological and physiological components is similarly lacking, (Smucker *et al.*, 1987) and these factors are critical to the understanding of a vine's responses to the environment. In order for the sink-soil-plant relationship to be understood, both the above and below-ground portions of the plant must be investigated (Upchurch and Ritchie, 1983).

To determine *in situ* root growth development and periodicity, a nondestructive method is required. Recent work (Smucker *et al.*, 1987) has demonstrated the efficiency of the minirhizotron system in agronomic crops. It allows accurate, repeatable measurements of a particular plant or plant population on a specific date and soil depth (Upchurch and Ritchie, 1983; Atkinson, 1980; Box *et al.*, 1989). This method was selected for test to determine its utility for studies on grapevines.

Seyval was selected as the plant material because it is a valuable hybrid grape cultivar, widely grown for white wine production in the Eastern United States (Reynolds *et al.*, 1985; Kaps and Cahoon, 1989) and it produces numerous large clusters which create a tendency to overcrop. This overcropping is the major problem of Seyval culture in cool climate viticultural regions and results in inadequate net photosynthesis (Pn) to meet the multiple requirements of fruit production, shoot and root growth, carbohydrate storage and tissue cold hardiness. Grapevine yield is determined by the number of

inflorescences per shoot and the number of fruitful shoots per vine (Bhargava and Sumner, 1987). Larger vines have more leaves exposed to the sun, which results in higher carbohydrate production levels in the grapevine (Howell, 1987; Striegler and Howell, 1991).

Flower-cluster or cluster thinning are currently employed to correct the excessive crop load. Flower-cluster thinning (FCT) removes excess flower clusters between spring foliation leafing out and bloom. Reynolds *et al.* (1986) reported that such thinning on Seyval blanc vines had several positive effects, with no negative effects to crop yield or fruit composition. The greatest effect was the reduction in the second crop (clusters produced on fruitful buds of lateral shoots). Bunch rot was reduced more with thinning 25 clusters/500 g of cane pruning than thinning 10 or 17 clusters/500 g of cane pruning (Reynolds *et al.*, 1986). By thinning, the powerful fruit sink is diminished and the leaf to fruit ratio is increased. In that work, differentiated clusters exhibit greater percentage fruit set, and large berries per cluster. To cluster-thin (CLT), entire clusters are removed after fruit set. This technique is essentially the same as FCT except for timing and appears to reduce the nutritional competition for the remaining berries. Morris *et al.* (1987) reported an increase in the number of berries per cluster on cluster thinned Seyval vines as compared to not thinned vines. Both thinning methods are labor intensive and expensive. Thus an alternate method for thinning to control overcropping is needed. One approach would be the use of vigor imparting rootstocks. Increased vigor may increase leaf area and make thinning less critical.

Unreported data from our field experiments suggest that 30% higher yields are

possible when Seyval is grafted to vigorous rootstocks. Root performance may thus become an important factor in successful Seyval culture, and grafting Seyval to a vigorous rootstock would provide an experimental basis to compare differences in root performance while also evaluating the above-ground response of the same vines.

The experimental approach was as follows: to examine the response of Seyval root systems *in situ* using the minirhizotron at approximately two week intervals, determining timing and quantification of root activity. Growth, yield and fruit composition measurements were also taken so that root growth phenomena could be compared with that of above ground organs.

Finally, a series of treatments which have been demonstrated to have an impact on growth and development of above ground organs (water stress, crop load and rootstock choice) were selected. Through this factorial approach, a range of stress combinations could be imposed on the vines and their impact measured. A key advantage in this work was access to a modern rain exclusion shelter (Martin *et al.*, 1988), which minimized irrigation control difficulties and improved the precision of the water status measurements when using the neutron probe (Chanasyk and McKenzie, 1986) to determine soil moisture content.

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CHAPTER I: REVIEW OF LITERATURE

Water stress. Plants experience many different environmental stresses (i.e. high or low temperatures, disease, pathogens, and unfavorable soil conditions), but water-deficit is probably responsible for the greatest loss in crop yields and plant growth (Kramer, 1983). When the plant water potential and turgor are reduced to a point where normal plant functioning is impaired, a plant is under water stress (Kramer, 1983). In general, as water stress increases, plant yields decreases (Hardie and Considine, 1976). The point at which water stress occurs depends on the type of plant.

Water stress studies with grapevines pose unique responses to drought stress. Grapevines have high water conductivity due to large xylem vessels and deep roots (up to 6 metes) (Smart and Coombe, 1983). With their deep roots, grapevines are more drought tolerant than other deciduous, woody fruit crops such as apples, pears, and prunes (Smart and Coombe, 1983; Atkinson, 1980). *Vitis vinifera* grapevines have been reported to osmotically adjust to water stress (During, 1984; Escamilla, 1985).Water stress has a primary impact on plant root systems, shoot growth and development and it is one of the most common stresses experienced by field-grown plants (Zhang and Davies, 1989). When plants are under water stress, many processes are affected (Sharp and Davies, 1979): 1) cell division (Hardie and Considine, 1976) and enlargement are inhibited (Hsiao, 1973; During, 1984; Nonami and Boyer, 1990); and 2) expansive growth (Hsiao, 1973; Westgate and Boyer, 1985; Hsiao and Jing, 1987; Bunce, 1990), CO_2 uptake (During, 1987), leaf extension and development (Sharp and Davies, 1979),

turgor (Hsiao and Jing, 1987) are also reduced by water stress. By contrast, root production (Freeman and Smart, 1976; Sharp and Davies, 1979), development of grapevine periderm and reducing sugars of fruit commonly increase (Matthews *et al.*, 1987).

Water potential is the fundamental measure of plant water status (Hsiao, 1973; El-Barkoriki, *et al.*, 1979). Leaf water potential (ψ_l) is dependent on the intrinsic properties of the leaf (i.e. the cuticle, mesophyll cells, and stomata), and environmental factors such as solar radiation and temperature (Smart, 1974a). It is commonly measured using a Scholander bomb or vapor pressure psychrometer. As the water stress of the vine increases, ψ_l becomes more negative (Smart, 1974a; Hardie and Considine, 1976). Generally, the ψ_l becomes more negative in the early morning, continues to decline to midday, and then becomes less negative later in the afternoon (Smart, 1974a). The threshold value of ψ_l for a change in stomatal aperture of *V. vinifera* L. is about -0.4 Mpa (Kriedemann and Smart, 1971; Smart, 1974a), with the critical value for stomatal closure occurring at about -1.3 Mpa (Smart, 1974a).

Root growth is less sensitive than shoot growth to water stress (Westgate and Boyer, 1985) and this decreased sensitivity may be due to the ability of the roots to accumulate solutes and maintain turgor (osmotic adjustment) (Sharp and Davis, 1979). Leaf cell walls harden, yielding slower growth in spite of turgor maintenance while root cell walls become more plastic and extensible (Hsiao and Jing, 1987). As water stress increases, root growth is less affected than shoot growth; shoot growth is, in turn, less affected than leaf growth (Hsiao and Jing, 1987; Boyer, 1988). Shoot growth in

grapevines is inhibited before water potentials in the leaf approach -1.3 Mpa (Smart, 1974a; Escamilla, 1985). When leaf growth is inhibited but not photosynthesis (per unit area of leaf), assimilates no longer being utilized by the leaves for growth may be transported to the roots (Hsiao and Jing, 1987). In maize, the root biomass of water-stressed plants increased relative to the adequately irrigated plants (Sharp and Davis, 1979). This observation also may be true with grapevines since Koblet and Perret (1982) found that root growth in potted vines of Pinot noir grafted on 5C was stimulated for vines treated with 2-4 weeks without water, as compared to well watered vines. During (1984) also reported increased root weight of potted Riesling vines under water stress compared to well-watered vines.

As water stress increases, shoot growth and water use of the vine decrease (Nonami and Boyer, 1990). Shoot and pedicel browning are usually the first signs of water stress (Gentry and Stout, 1971). Stress symptoms in *V. vinifera* leaves are initially expressed at -0.4 MPa. If the water deficit continues, tendrils, leaves and berries may abscise and there are reductions in shoot growth (Matthews, *et al.*, 1987; Smart, 1974a), rate of fruit growth (Matthews *et al.*, 1987), and vine yield (Buttrose, 1971; Carbonneau and Casteran, 1979). Berry death due to desiccation is less likely to occur after it exceeds a diameter of 4 mm (Hardie and Considine, 1976).

Photosynthesis. The efficiency of photosynthetic conversion by agricultural crops is about 1-2% (Smart, 1974b), but it is the most important physiological process of plants (Winkler, 1974). Environmental, and physiological variables affect the efficiencies of both photosynthesis and translocation in grapevines.

The leaf is the main photosynthetic organ of the plants (Smart, 1974b). Small, rapidly expanding leaves cannot meet their photosynthetic demands for growth and rely on importation of assimilates. Full expansion of leaves of *V. vinifera* (Sultania) is completed approximately 30-40 days after unfolding, and senescence (in Australia, in full sun) occurs 4-5 months after unfolding. Within a grapevine canopy, leaves can be divided into two groups: those which receive only diffused light (shaded leaves) and those which receive both diffused and direct sunlight (exterior, exposed leaves) (Smart, 1974b). Most photosynthesis occurs in exterior leaves receiving direct light. Photosynthesis in shaded, interior leaves is inhibited due to rapid attenuation to low flux densities (Kriedemann and Smart, 1971; Smart, 1974b). When leaves achieve full size, photosynthetic activity peaks. Absorption of incident radiation, leaf area, and chlorophyll content all increase with age up to a point. Photosynthetic activity declines as the leaves approach senescence usually, days after full expansion.

Photosynthate movement from a leaf changes during shoot growth (Quinlan and Weaver, 1970; Motomura, 1990). Young, and rapidly growing leaves are strong importers of photosynthate from other parts of the vine, and are not photosynthetically self sufficient (Kriedemann, 1968). The grapevine leaf is an importer of photoassimilates until it is about half of its full size (Hale and Weaver, 1962). When the leaf starts to export photosynthates, the direction is acropetal for 1 or 2 days. When an additional leaf is initiated, the direction of the photosynthates translocation is bidirectional. With continued growth, and the production of new leaves, the direction of photosynthate movement becomes predominantly basipetal (Quinlan and Weaver, 1970). When the

leaves above a cluster begin to translocate photosynthates basipetally, most of the movement continues in that direction. Leaves below a cluster become bidirectional after berry shatter and continue translocating photosynthates bidirectionally throughout fruit ripening. After fruit set, many of the photosynthates are translocated basipetally (Hale and Weaver, 1962).

The growth of the grapevine can be modified by water stress to influence vine photosynthesis (Smart, 1974b; Hardie and Considine, 1976; Liu *et al.*, 1978), vine vigor (El- Barkoriki, *et al.*, 1979; Carbonneau and Casteran, 1979; Nonami and Boyer, 1990), transpiration (Gentry and Stout, 1971; Smart, 1974b), berry quality (Swift *et al.*, 1973; Hardie and Considine, 1976), vine yield (Buttrose, 1971), and abscisic acid content of leaves (Nomami and Boyer, 1990). The rate of photosynthesis is the highest when water deficit is low or absent (Smart and Coombe, 1983). Water stress may influence grapevine photosynthesis directly, or indirectly: directly, by impairment of the photosynthetic apparatus of the vine, and limiting the biological process; or indirectly, by regulating stomata aperture and reducing the supply of carbon dioxide to the vine (Kliewer *et al.*, 1984).

Stomatal conductance, and CO^2 assimilation are directly related (Liu *et al.*, 1978). A lowering of stomatal conductance yields a reduction of photosynthesis and $C0_2$ assimilation (Freeman *et al.*, 1982). Stomata close earlier in the day (0800 hr) in water stressed Shiraz vines than non-stressed vines (1145 hr), with little difference in water potential at noon. Stomata close at about -1.3 to -1.6 MPa (Smart, 1974b; Liu *et al.*, 1978). Development and density of stomata varies with growing conditions in *Vitis*

labruscana Bailey. Mature leaves in field grown vines have more stomata than potted vines (Liu *et al.*, 1978). In Concord vines, stomata close at approximately -1.3 MPa in potted vines, but remain open at approximately -1.6 MPa in field-grown vines (Liu *et al.*, 1978).

Abscisic acid. The plant hormone abscisic acid (ABA) can modify photosynthesis of *V. vinifera* in grapevines. The concentration of ABA increases in the leaves of many cultivars (Concord, Nampa Gamay, and Carignane) when the vines are exposed to water stress (Loveys and Kriedemann, 1973; Kliewer *et al.*, 1984). ABA levels increase during drying cycles and return close to original pre-stress levels when water is restored (Loveys and Kriedemann, 1973). This suggests that stomatal response to water potential is related to ABA levels (Liu *et al.*, 1978).

Zhang and Davies (1987), suggested that the roots of Commelina grapevines and pea plants have the capability to synthesize ABA in the roots and then transport it to leaves on the shoots via the transpiration stream for stomatal control. In sunflowers and maize (Zhang and Davies, 1989, 1990) the roots are the primary plant sensors in shallow, drying soil, and signals are sent from the roots to the shoots. The signals restrict leaf stomatal conductance and leaf growth rate. If the soil drying continues, the signals become stronger, resulting in wilting of older leaves.

ABA may play a role in fruit ripening (Hale and Coombe, 1975). Endogenous concentrations of ABA increase during the ripening process of many fruits (apples, citrus, and grapes). Endogenous ABA concentration begins to increase shortly before veraison. Any treatment which delays veraison will inhibit the increase of ABA.

Ripening time of Doradilo grapes is advanced (four days) when sprayed with ABA for five consecutive days, beginning 11 days before veraison (Hale and Coombe, 1975) while earlier or later applications have no effect. The exogenous ABA applications increases endogenous ABA concentrations. Application of benzothiazole-2-oxyacetic acid (11 days before veraison) depresses endogenous concentrations of ABA, and delays veraison (Hale and Coombe, 1975).

Roots. Zobel (1990) describes a plant root system as a colony or population of types of roots, each type with a different function. The root is divided into distinct areas (Fig. 1): the root tip; the absorption zone; and the conduction zone (Pratt, 1974). The root tip is the youngest portion of the root where new cell tissue forms, and root elongation takes place. The absorption zone, is where root hairs are formed, and a considerable portion of water and nutrients are taken in. The remainder of root is the conduction zone (Pratt, 1974) and is used by the vine for storage of carbohydrates, water and nutrient movement, and support. Suitable sites for root distribution are achieved by the continuous exploration and re-exploration of the rhizosphere by the roots (Zobel, 1990).

The roots of the grapevine consists of all below-ground parts of the vine, as well as some roots that develop from the above-ground portion of the stem (Winkler, 1974). Branch roots develop from pericycle cells in the interior of the roots (Winkler, 1974; Pratt, 1974); primary adventitious roots from the node develop lateral secondary roots. Lateral secondary roots develop tertiary roots and higher order branch roots. Root hairs were once thought to absorb the majority of water from the soil (Perold 1927), but

Freeman and Smart (1976) suggested that both suberized and new, unsuberized roots must absorb water to prevent vine water stress because grapevine roots begin to grow considerably later than shoots.

Crop load. Crop regulation may be done by either flower-cluster or cluster thinning (as described in the Introduction), by pruning (Winkler, 1974), and by balanced pruning (Bell *et al*, 1958). Thinned vines produce well, fruit quality is good, vigor and capacity are high, but the labor expense tremendous compared to non-thinned vines. On large cluster cultivars, pruned, but non-thinned vines do not produce as well as thinned vines, nor is the fruit quality as good, but is less labor intensive. A combination of flower cluster thinning and pruning improves fruit quality, vine capacity; develops vines with good vigor and good capacity (Winkler, 1974) at a reasonable cost (Howell, *et al.*, 1987). Balanced pruning was introduced by Partridge in 1927 (Bell *et al.*, 1958) and is also currently used to correct excessive crop loads. This method of pruning attempts to ensure that vines consistently produce an acceptable quality crop load without negatively reducing vegetative yield as indicated by weighing dormant cane cuttings. When that occurs the vine has been balanced pruned. Larger vines are capable of producing more crop than smaller vines and are thus pruned to retain more buds. Smaller vines are pruned to fewer fruitful buds. By this method of pruning smaller vines, problems associated with the production of excess crop (overcropping) will be minimized.

Overcropped vines will often have a smaller crop the following year (Winkler, 1974). Such vines have poor fruit composition, diminished vine capacity, and eventually reduced fruitfulness (Winkler, 1974). A larger vine has a greater growth potential than

a smaller one, but may produce fewer fruitful buds if excessive growth results in internal shading (Winkler, 1974). Heavy crop load reduces percentage of soluble solids and pH, increases acidity and suppresses subsequent year's yield of Niagara (*V. labruscana*) as a result of reduced node fruitfulness (Morris *et al.*, 1987).

Maturation of seeded grape berries are divided into three periods: rapid growth, depressed growth, and final swell (Pratt, 1974). Two periods of rapid berry growth are separated by a period of slow growth, described as a double sigmoid curve (Matthews *et al.*, 1987). Berry size is a function of cell size and cell number (Harris *et al.*, 1968). The first period of berry growth is due to cell division and expansion. The second period of growth is a resting or lag phase. While the third period of growth is due to cell expansion alone (Harris *et al.*, 1968; Hardie and Considine, 1976).

The major compositional changes in the berry occur during ripening. These include higher reducing sugar content and lower acid content. During the first growth period, the berry accumulates malic and tartaric acids. During the second growth period the overall growth rate of the berry slows; the endocarp hardens, and the embryo develops rapidly. During the third growth period, the berry softens, accumulates sugars, losses acidity, and in pigmented cultivars, develops anthocyanin.

Water stress affects berry growth, but the phase of berry growth in which the water stress occurs is also important (Hardie and Considine, 1976; Richards, 1986) and may reduce vine yield (Hsiao, 1973; Chevone *et al.*, 1990). The greatest sensitivity occurs during the lag phase of berry growth (Hardie and Considine, 1976). Loss of berry moisture during this phase causes excessive softening in the berries, deleteriously

affecting taste and salability (Gentry and Stout, 1971) but may enhance the development of anthocyanin pigments in the berry skin (Hardie and Considine, 1976). Water stress also has been found to increase pH in grape (McCarthy and Coombe, 1985). A mild water stress may enhance berry sugar accumulation; alternately, a more severe water stress may delay berry sugar accumulation due to reduced photosynthetic rate (Smart and Coombe, 1983). In general, water stress reduces berry number (fruit set), berry weight, cluster weight (Smart and Coombe, 1983) and hastens berry maturity (McCarthy and Coombe, 1985).

Fruit growth becomes an increasingly competitive photoassimilate sink compared to vegetative growth in grapevines as the berries mature (Richards, 1986). Ten to 14 days before bloom, the cluster is a weak sink compared to the shoot tip and the parent vine. Axillary buds and tendrils are weak sinks compared to the developing cluster. Compared to fruit clusters, the shoot tips and parent vine are powerful sinks during flower development, but weak during fruit set (Hale and Weaver, 1962).

Rootstocks. Rootstocks have a direct effect on vine size and water uptake (Howell, 1987; Striegler and Howell, 1991), and rootstocks to which vines are grafted differ in their drought tolerance (Spiegel-Roy *et al,* 1971; Bravdo *et al.*, 1972; El-Barkoriki, *et al.*, 1979; Smart and Coombe, 1983; Pongracz, 1983; Carbonneau, 1985, Howell, 1987). The rootstocks 'Riparia Gloire', '5BB', 'SO 4', '5C', 3309 C', '3306 C', '101-14', '1616 C' are reported to be drought sensitive (Howell, 1987). The rootstocks '110 R', '140 Ru' are very drought tolerant, with rootstocks '1103 P', '41 B' and others reported as moderately drought tolerant (Howell, 1987).

There are differences in root structure among different species of *Vitis*. Some, such as the *V. riparia* have roots that are shallow, spreading, thin, and fibrous which grow well in moist soils. The *V. riparia* is not reported to be drought tolerant (Howell, 1987). The *V. cordifolia* has thick roots which grow well in dry soils (Pongracz, 1983). The *V. rupestris* has roots that are less fibrous, but deeper penetrating than *V. riparia*, and is slightly more drought tolerant (Howell, 1987). The *V. berlandieri* have roots that are less branched than *V. rupestris* and are deeply rooting; The species is reported to be very drought tolerant (Howell, 1987). The *V. champini* have hard, wiry roots that are deeply penetrating. The species is also reported to be very drought tolerant (Howell, 1987). These differences may be attributed to the water absorbency activity of the rootlets (Carbonneau, 1985).

Rootstocks have a direct and indirect effect on vine capacity (Pongrancz, 1983; Striegler and Howell, 1991; Candolfi-Vasconcelos *et al.*, 1993). Vine capacity is defined as the ability of the vine for total production (Winkler, 1974), and may be limited by soil (Perold, 1923), rootstock, pruning weight (McCarthy and Cirami, 1990), vine health when it is pruned (Perold, 1927), vine spacing (Kimball and Shaulis, 1958), pruning severity (Winkler, 1974), and vine size (Partridge, 1926). Direct effects include water and mineral nutrient uptake, production of plant growth regulators and storage of carbohydrates (Striegler and Howell, 1991). Indirect effects include lowered berry sugar content associated with more vigorous rootstocks (Howell and Striegler, 1991) and grafting vines to a vigorous, pest-resistant rootstock (Wolf and Pool, 1988).

Indirect effects also include vine size modifications, such as increased or reduced

internal canopy shading. At low light intensities associated with increased internal shading, photosynthetic assimilates may be insufficient for developing ovaries (Roubelakis and Kliewer, 1976). Approximately 10 to 12 cm^2 leaf area is needed to adequately ripen 1 gram of fruit in terms of soluble solid accumulation (Kliewer and Antcliff, 1969). In shaded canopies, berries have reduced composition values based on lower reducing sugar accumulation (Koblet and Perret, 1982), and higher acid content (Shaulis and Smart, 1974). Percent fruit set and ovule development are higher in *V. vinifera* grapevines at high light intensity (above 1000 PPF) than at low light intensity (500 PPF).

Clearly, crop load, moisture status and rootstock can individually influence vine growth and productivity. They may also act in concert. These influences may be direct as in water stress and shoot extension or indirect as in water stress: photosynthesis: and fruit composition. For these reasons, this study to evaluate vine performance of young, variably fruited Seyval grapevines, grafted and ungrafted under adequate and drought conditions was organized and initiated.

Goals of This Study

For the interactions of water stress, rootstock and crop load to be understood, a factorial experiment was designed to test the relative strengths of these affects on vine and root growth and development.

The goals of this study were:

1. to concomitantly evaluate the effects of water stress, rootstock, and crop load on and carbohydrate partitioning to above and below ground portions of newly established Seyval grapevines.
2. to determine how growth responses vary among different root systems and different parts of the vine.
3. to evaluate the effects of water stress, rootstock and crop load on vine gas exchange.
4. to evaluate the efficiency of the minirhizotron system for study of root growth dynamics under the conditions imposed in goals 1-3.

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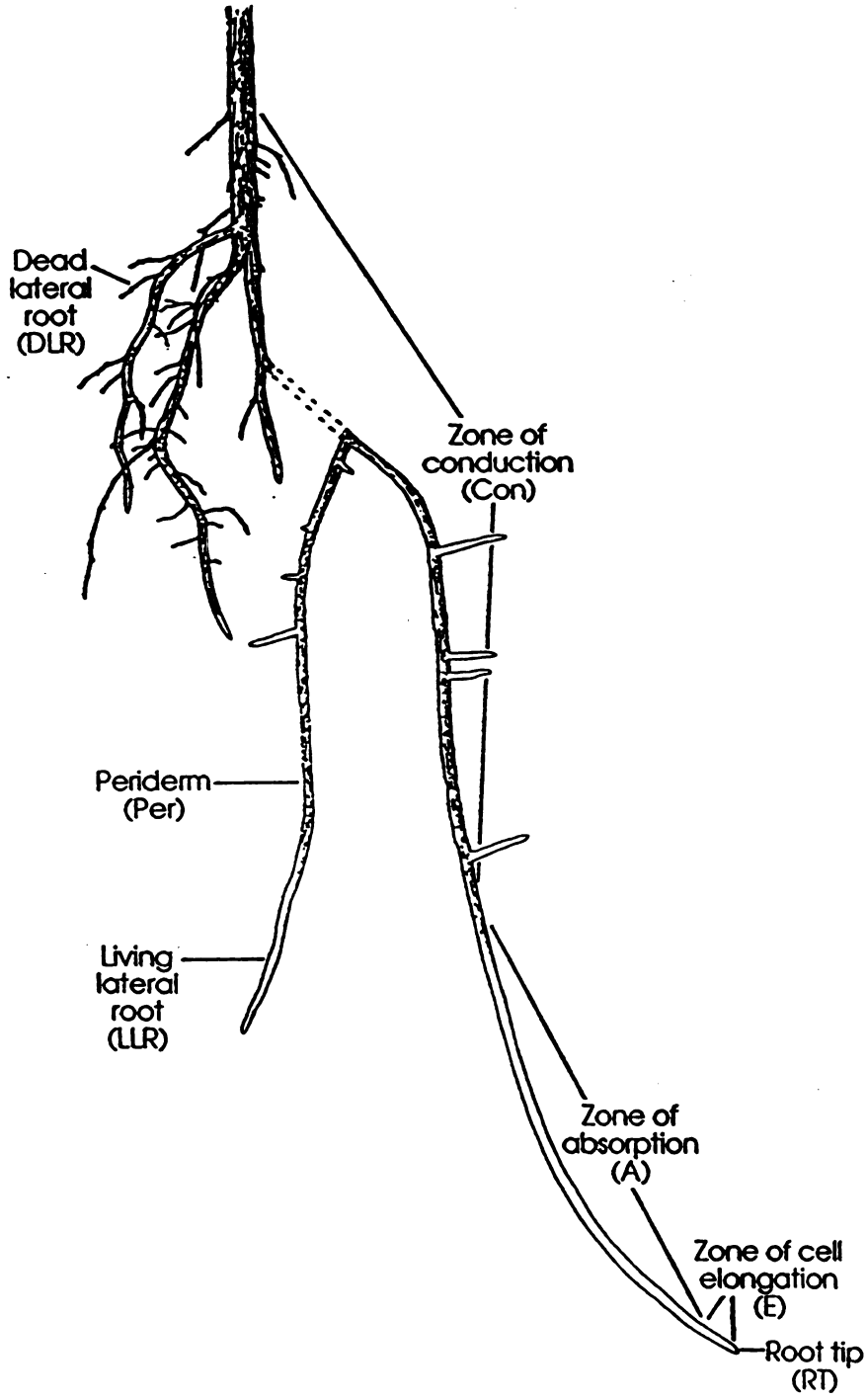
Caption for Figure

Figure 1. Root of Seyval grapevine. Redrawn from Pratt, 1974. Abbreviations: A, zone of absorption; Con, zone of conductance; DLR, dead lateral root; E, zone of elongation; LLR, living lateral root; Per, periderm; RT, root tip.


Dead lateral root (DLR)
Zone of conduction (Con)
Periderm (Per)
Living lateral root (LLR)
Zone of absorption (A)
Zone of cell elongation (E)
Root tip (RT)

CHAPTER II: RESEARCH NOTE: A MINIRHIZOTRON SYSTEM FOR *In Situ* ROOT OBSERVATION STUDIES WITH SEYVAL GRAPEVINES

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ABSTRACT

Root distribution and dynamics of Seyval grapevines were measured *in situ* by the nondestructive minirhizotron and portable microcamera system. Transparent polybuterate tubes were inserted at 45 degrees to the soil surface within the rows of vines 30 cm from the base of each vine at intervals of 60 cm. Polybuterate tubes were installed to a vertical depth of 127 cm in a Kalamazoo loam soil (fine-loamy, mixed, mesic Typic Hapludolfs). Root numbers in each 2.16 cm^2 of the upper surfaces of the transparent tubes, at intervals of 1.2 cm, were counted from video recordings of the root images. This method of observing root dynamics was used to determine the depth, development, distribution, and turnover rates of roots of grapevines containing 0 and 6 clusters of fruits per vine which were subjected to optimum and deficit soil water conditions.

KEY WORDS: Minirhizotron, non destructive assays, root number, root distribution, and root dynamics.

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INTRODUCTION

Traditional methods of root research, especially with large plants such as grapevines, are difficult to access (6,8), expensive (12), tedious and time consuming (1,2,14), and highly variable (9). Hence, there is a need for improved methods for studying root numbers, turnover (3,13,15,20), and dynamics (17).

Nondestructive methods of root observation are preferable because they allow repeated observations of a particular plant root at a specific date, field location, and soil depth. However, many studies have been limited to hydroponic (14) or polyethylene systems (10) which do not simulate root growing conditions in soil media. Our system for nondestructive characterization of plant root growth *in situ* was to incorporate the minirhizotron micro-video camera system described by Upchurch and Ritchie (17) as modified by Ferguson and Smucker (5). Accurate measurements of the same plant root system can be accomplished by a microvideo color camera for a period of at least three

years providing the tubes remain transparent and maintain excellent contact with the surrounding soil (1).

The purpose of this study was to evaluate root depth and density responses to fruit loading of vines growing under low soil-moisture conditions using the nondestructive minirhizotron system. These results are used to estimate root dynamics and turnover rates when individual root counts are compared over time and at multiple depths.

MATERIALS AND METHODS

The experiment was conducted at Kellogg Biological Station, Battle Creek, Michigan, on a Kalamazoo type soil (fine-loamy, mixed mesic Typic Hapludalf) located in an automated rain-exclusion shelter (18). Two-year old Seyval grapevines (Seyve-Villard 5-276) grafted on 5BB; Seyval: and Seyval own rooted rootstocks were root pruned to 18 cm, and planted on May 22, 1989. Planting distances were 0.6 m within rows and 0.9 m between rows. Vines were managed to a single trunk, with two spurs. Two buds per spur were allowed to develop, obtaining a modified pendlebogen trellis system. Vines were drip irrigated at 10 liters per plant per week for 60 days after planting.

Experimental plots were completely randomized, with five replications (one plant representing one replication) per treatment. Treatments included vines which maintained 0 or 6 clusters, and were irrigated with either 10 liters of water per plant per week (optimal), or 2.5 liters of water per plant per week (drought stress). Irrigation treatments were initiated 60 days after planting.

One week before planting, the transparent polybuterate tubes (0.05 x 1.82 m having a wall thickness of 0.003 m) were inserted at 45 degree angles to the soil surface and parallel to the vine row; by the methods described by Box et al. (2) using a trailer mounted Giddings hydraulic soil probe (7). This installation technique insures an excellent minirhizotron-soil contact (2,3), and reduces the probability of roots following the soil-tube interface (9). The tube must contact the soil tightly enough to minimize voids at the soil-tube interface, but the tube surface should not be blurred by inserting it into a hole that is too small which may be a problem in wet clay-textured soils (8). A 30 cm section of the tube was left above-ground, painted with flat black enamel paint to exclude light and then repainted with flat white enamel to reduce heat transfer to the soil. An index notch was recessed into the upper surface of the above-ground portion of the minirhizotron tubes which served as a reference for the microvideo camera assembly (5). A rubber stopper inserted into both ends of each tube protected the internal portions of the minirhizotron. The top could be opened for frequent measurements by the microvideo camera assembly (5).

A portable control package for the camera system consisted of a 12-v D.C. power source, microcomputer, Timex video recorder, Panasonic, and control for the Circon (3) microvideo color camera assembly which were enclosed in a water and dust-tight case mounted on wheels. Minirhizotron tubes were swabbed with absorbent cotton to remove any condensation before each measurement. The microvideo camera was inserted to the lowest root depth of the tube, the tube number, date, time, and starting depth were video recorded and the camera was retracted up the minirhizotron tube at 1.2 cm intervals

every three seconds. The camera records an image "window" 2.16 cm^2, on the upper portions of the tubes, at each interval on the index handle (Fig. 1). Data acquisition required approximately 10 minutes per tube for an individual operator in the field. The number of roots per three-second picture are counted on a monitor in the laboratory and recorded using a computer program "Minisort". Treatment codes are assigned to each tube number, the coded files are then transferred to a statistical package or a statistical and graphics package PlotIt (11) and graphed.

RESULTS AND DISCUSSION

Root dynamics of grapevines were monitored every two weeks for the duration of the two-year experiment. Figure 2 shows the root distribution patterns for Seyval grapevines at 162 days after planting during the first season. More roots were observed in the soil profile from 40 cm to 70 cm for grapevines where the fruits had been removed. This may have resulted from the greater root growth in the soil profile having greater soil moisture during the water deficit treatment. In contrast, total numbers observed for vines with fruits in the upper 70 cm of soil, were 14.5% of the numbers observed for vines without fruits (Fig. 2). These differences in root growth responses to fruit load were not observed for the water Control treatment (data not shown).

The minirhizotron method of root evaluations provides many advantages over traditional and more destructive methods of root analysis. With this method, root measurements can be made *in situ* on the same vine throughout its growth period without destroying the sample (1,9,17). Consequently, accurate and repeated measurements of

the same plant root system are possible (9) and it is time and labor efficient (3). It provides reproducible measurements of root growth and distribution in the soil, changes in activity of root systems, root density, and changes in plant root depth over time (9,16).

Currently, minirhizotron tubes can be installed to depths of up to 3 m (19). Tubes may be installed before or after planting. If tubes are installed several weeks before planting they are able to seat well before planting the crop (1). When tubes are installed in mature vineyards the tractor-mounted soil Giddings probe should be able to cut through most of the large roots of grapevines associated with mature stands. Problems may occur when installing tubes through clay soils due to smudging of the tube surface (1,8) or the expanding and contracting properties associated with soils containing $> 55\%$ expanding and contracting clay minerals.

Practical applications of the minirhizotron system have been discussed considerably for agronomic crops (1,8,17). Conceivably, root analysis with the minirhizotron may become as routine as the study of the above-ground portion of field-grown plants (3). A special interest for our research with Michigan grapevines are seasonal changes in root growth and nutrient uptake and the source-sink relationships critical to long term effective viticulture. The minirhizotron system promises to be a valuable tool for root observation studies of grapes and many other crops (1,2,3,5,8,9). In conclusion, the minirhizotron system is a nondestructive method of root observation and appears to be an effective method for measuring grapevine root distributions through the soil profile of loam soils.

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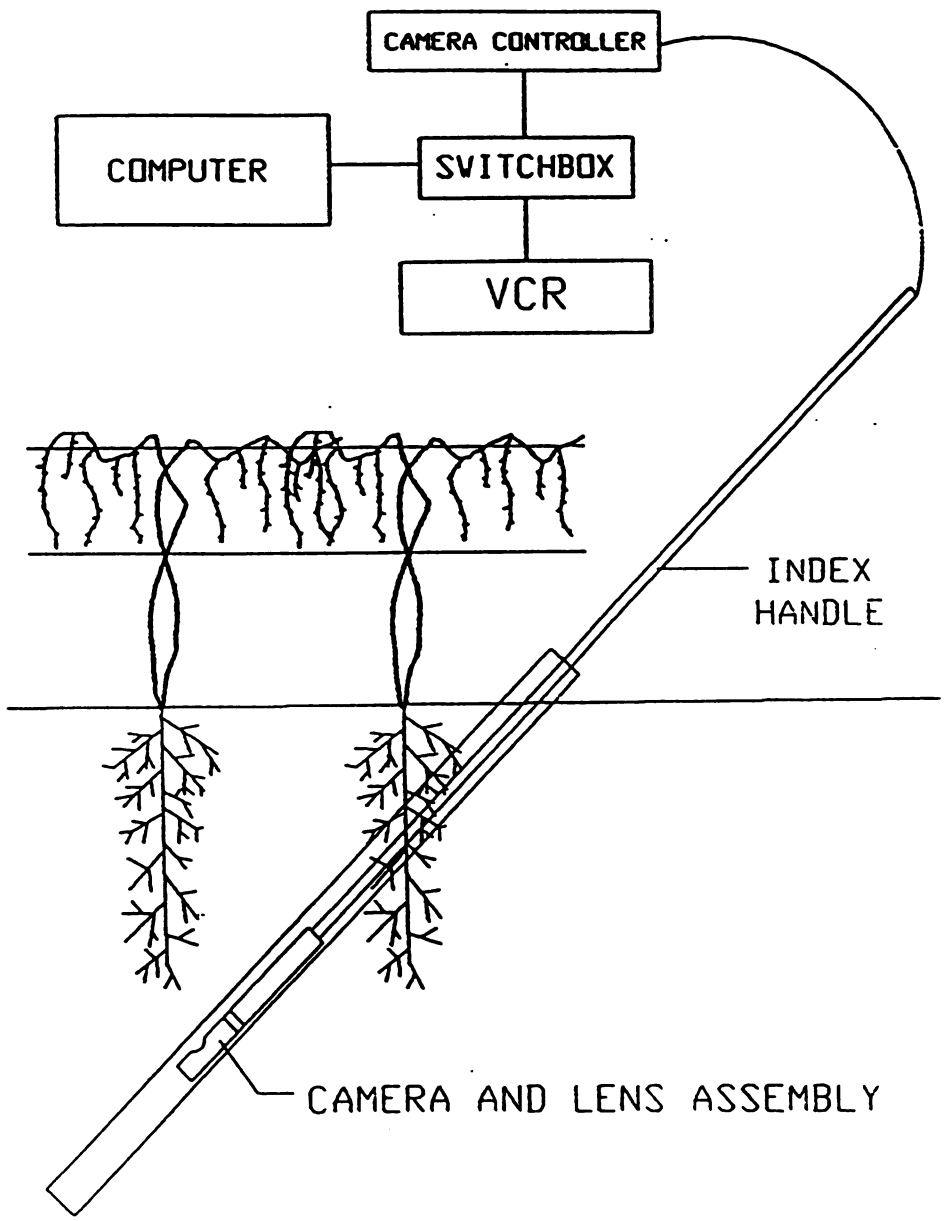
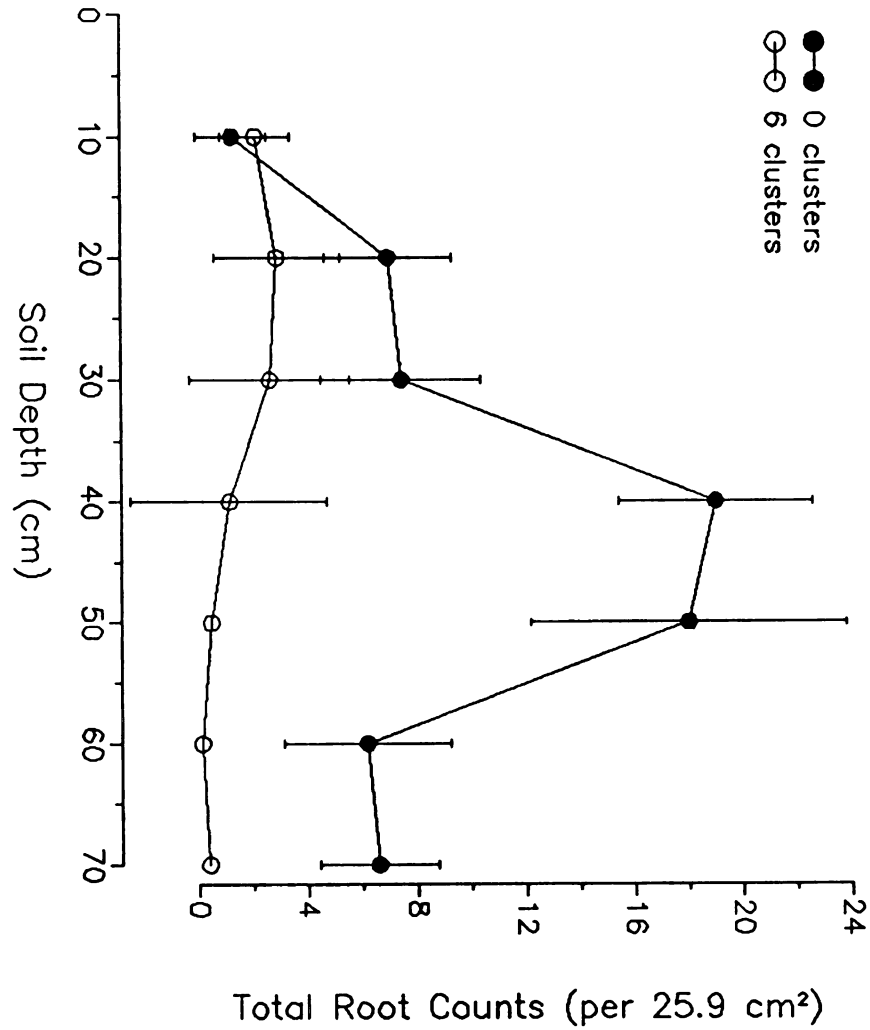
CAPTION FOR FIGURES

Figure 1. Diagrammatic representation of the microvideo camera assembly, including the control system, indexing handle and minirhizotron tube installed at 45 degrees below the plants.

Figure 2. Root distribution pattern of drought-stressed grapevines containing 0 and 6 fruit clusters per vine, to a soil depth of 70 cm. Vertical bars represent SE.


CAMERA CONTROLLER
COMPUTER
SWITCHBOX
VCR
INDEX
HANDLE
CAMERA AND LENS ASSEMBLY


0 clusters
6 clusters
Soil Depth (cm)
0
10
20
30
40
50
60
70
0
4
8
12
16
20
24
Total Root Counts (per 25.9 cm²)

CHAPTER III: EFFECTS OF WATER-STRESS, ROOTSTOCK, AND DEFRUITING ON VINE AND ROOT GROWTH IN SEYVAL GRAPEVINES

ABSTRACT

This experiment was conducted to evaluate interrelationships between differing crop loads and water stress on carbohydrate partitioning for above and below-ground tissues of Seyval grapevines grafted on three different rootstocks. Fine root development and depth were determined by quantifying root images from video recordings taken to depths of 80 cm at approximately 2 week intervals throughout the growing season. Two-year old own-rooted Seyval grapevines, and Seyval grafted to 5BB and to Seyval were grown under a rain exclusion shelter and provided with 10 or 2.5 liters of water/plant/week. Treatments were cropping level, either 0 or 6 clusters per vine. Shoot length, number of mature nodes, leaf area and leaf dry weight of vines under high cropping level were reduced compared to vines growing under the low cropping level; so was root number and depth of penetration. Conditions of low soil-moisture resulted in carbohydrate partitioning in favor of the clusters at the expense of the roots, and carbohydrate partitioning in favor of the roots at the expense of the above-ground vegetation.

INTRODUCTION

There is a need to quantify numerous morphological and physiological components of roots (Smucker, 1990) and to understand interrelationships between root function and development (Glen and Welker, 1992). Unfortunately, most quantitative studies of roots require destructive methods using root weight to assess the total amounts in the soil (Atkinson, 1980). Although there has been interest in the effects of soil-water content on plant growth (Natali *et al.*, 1985; Zobel, 1990; Proebsting, 1989; Ranny *et al.*, 1991), the importance of root performance on shoot growth and crop production (Head, 1969; Atkinson, 1980), and estimates of root dynamics to be used to predict carbon balances of the plant (Smucker 1990), little is known regarding *in situ* plant root growth (Upchurch and Ritchie, 1983; Feldman, 1984; McLean, 1992). Clarification of sink and soil-plant interactions regarding water stress and fruiting is problematic due to technical problems associated with extended plant root studies (Glen and Welker, 1992). However, such studies are crucial to our understanding of roots.

In order for the sink-soil-plant relationships to be understood, both above and below portions of the plant must be investigated (Upchurch and Ritchie, 1983). To follow fine root development and growth periodicity easily, nondestructive, observation window methods such as the minirhizotron system are preferable because they allow accurate, repeatable measurements of a particular plant at a specific date and soil depth (Upchurch and Ritchie, 1983; Atkinson, 1980; Box *et al.*, 1989; McLean *et al.*, 1992). The purpose of this investigation was to evaluate the interactions between water stress, rootstock and crop load on carbohydrate partitioning to the above-and below-ground

portions of Seyval (Seyve-Villard 5-276) grapevines during vineyard establishment and to determine how the growth responses vary among different root systems and different parts of the vine.

Seyval was selected as plant material for several reasons: 1) it is a valuable French-American hybrid grown for white wine production in the Eastern United States; 2) it is difficult to grow in Michigan due to the vine's propensity to produce large clusters and to produce a second crop on fruitful primary buds on lateral shoots (Howell *et al.*, 1991); and 3) field experiments (unpublished) showed that 30% higher yields are possible when Seyval is grafted to vigorous rootstocks. These latter data suggest that root condition influences yield, berry weight, cluster weight, vine size, cluster number and bud fruitfulness.

The viticultural goal is to produce a stronger root and shoot system for the vine, and thus increase yield of grapevines. This paper reports *in situ* investigations with a microvideo system of quantifying total live roots visible through minirhizotron observation tube. The relationship between water-stress, rootstock and crop load and the above-and below-ground portion of Seyval grapevines were assessed.

MATERIALS AND METHODS

Location and Soils. This experiment was conducted at the Kellogg Biological Station, Battle Creek, Michigan, on a Kalamazoo type soil (fine-loamy, mixed mesic Typic Hapludolfs) located in an automated rain-exclusion shelter (Martin *et al.*, 1988).

Minirhizotron. Roots of grapevines have a low density compared to deciduous

fruit trees (Atkinson, 1980), so minirhizotron tubes were installed directly in the row, 30 cm from each vine to maximize observations of fine roots (Smucker, 1990). One week before planting, transparent polybuterate tubes (0.05 x 1.82 m having a wall thickness of 3 mm) were inserted in the soil. Each tube was inserted at a 45 degree angle to the soil surface and parallel to the vine row, using the methods described by Box *et al.* (1989) and a trailer- mounted Giddings hydraulic soil probe. This installation technique insured an excellent minirhizotron-tube-soil contact (Box *et al.*, 1989) and minimized the likelihood of fine roots following the soil-tube interface (McMichael *et al.*, 1987). The tube must contact the soil tightly enough to minimize voids at the soil-tube interface, but the tube surface should not be blurred by inserting it into a hole that is too small, which can be a problem in wet clay-textured soils (Maertens, 1987).

A 30-cm section of the tube was left above-ground, painted with flat black enamel paint to exclude light, and then repainted with flat white enamel to reduce heat transfer into the soil. An index notch was recessed into the upper surface of the above-ground portion of the tubes which served as a reference for the Bartz microvideo camera assembly (Santa Barbara, Calif.) using the modified indexing handle as described by Ferguson and Smucker (1989). A rubber stopper inserted into both ends of each tube protected its internal portions. The top could be opened for frequent measurements by the microvideo camera assembly as described earlier (McLean *et al.*, 1992).

Plant Materials. Two-year-old Seyval grapevines (Seyve-Villard 5-276) were grafted on Kober (5BB), Seyval (S/S), or own rooted Seyval (OR). The vines were root pruned to 18 cm and planted on May 22, 1989. Planting distances were 0.6 m within

rows and 0.9 m between rows. Vines were trained to a single trunk with two spurs. Two buds per spur were allowed to develop, obtaining a modified pendlebogen trellis system (a low-head at the bottom wire).

Irrigation. The first year, vines were drip irrigated at 10 liters per plant per week for 60 days after planting (DAP), starting on May 22, 1989. The second year, vines were drip irrigated at the same level and duration for 60 days, starting on May 22, 1990. Based on Kellogg Biological weather data from the three previous growing seasons, 60 days was an adequate time to irrigate the vines prior to implementing the water stress. Experimental plots were completely randomized into five, single-vine replications per treatment.

Treatments. In 1989, treatments included vines which were defruited at set or maintained at 6 clusters and were irrigated 60 DAP (July 22, 1989) with either 10 liters of water per plant per week as a control, or 2.5 liters of water per plant per week as a drought stress. In 1990, treatments included vines which were defruited at set or maintained at the maximum clusters (to a maximum of 6) and were irrigated 60 DAP (July 22, 1990) with either 10 liters of water per plant per week, or 2.5 liters of water per plant per week. Due to excessive cool weather during the early summer, the drought-irrigation level was reduced from 2.5 to 1.8 liters of water per plant per week beginning on 92 DAP (August 22, 1990).

Soil-Water Content and Matrix Potential. Soil-water moisture data were obtained by a model 503DR hydroprobe, neutron depth moisture gauge (NP). The NP measured sub-surface soil-moisture through aluminum access tubes, with 5 replications, to a

maximum depth of 75 cm in 25 cm cable stop intervals. The NP was calibrated to field conditions according to the methods of Chanasyk and McKenzie (1985). The NP recorded a current standard 16 second count format. This count was then changed to soil-water % moisture by the formula:

$$\theta = 2.42 \cdot 10^{-5} \text{ (counts)} + 0.004$$

$$\theta = 2.42 \cdot 10^{-5} \text{ (counts)} - 0.0036$$

Where "θ" is the soil volumetric moisture content, "counts" is obtained directly from the NP, and 0.004 is the coefficient of a sandy loam soil (depth 0-50 cm of a Kalamazoo soil); 0.0036 is the coefficient of a sandy soil (51-75 cm of a Kalmazoo soil). Matrix potential was derived from θ by the formulas:

Soil depth = 25 cm: if $\theta < 0.289$ then $y = 8.84\theta + 2.65$

if $\theta \geq 0.289$ then $y = 62886.19 \cdot 10^{3}\theta\, e^{-70.37\theta}$

Soil depth = 50 cm: if $\theta < 0.236$ then $y = -10.51\theta + 2.58$

if $\theta \geq 0.236$ then $y = 29190.94\theta \cdot e^{-54.07\theta}$

Soil depth = 75 cm: if $\theta < 0.112$ then $y = 24.51\theta + 2.84$

if $\theta \geq 0.112$ then $y = 0.04\theta\, e^{-12.09\theta}$

Where "y" is matrix potential (MPa) and "θ" = θ ($0 \leq \theta \leq 1$).

Leaf Water Potential (ψ_l). The ψ_l was measured before sunrise with a Scholander-type pressure bomb on 101, 488, and 502 DAP (October 4, 1989, October 6, 1990 and October 28, 1990, respectively). Five fully expanded leaves per treatment were excised with a razor and placed (within 30 seconds) so that the leaf mid rib extended from the sealed chamber of the pressure bomb. The air pressure was recorded

when a small amount of xylem exudate appeared on the cut surface of the excised tip of the petiole. A rubber gasket was used to minimize leaking of the compressed air from the petiole when the measurements were recorded.

Statistical analysis. Analysis of variance (ANOVA) was made using the PC version of SAS statistical software (SAS Institute Inc., Cary, N.C.), using a general linear model (GLM) procedure for total fine root numbers per vine. Analysis was performed at individual depths of 0-80 cm, as well as on shallow fine root totals (0-40 cm), deep total fine root numbers (40-80 cm), and combined total fine root numbers (0-80 cm) to identify trends in root periodicity as well as differences among treatments at different soil depths. Before total fine root numbers were analyzed they were processed by an "Outlier" program. The program compares total fine root numbers in each tube at a given depth with all other tubes of the treatment. The program disregards any total fine root numbers which were beyond two standard deviations from the mean and replaces those values with the mean of the remaining tubes, and acts as a low pass filter of total fine root numbers (values). The program allows low values to pass through, while modifying excessively high values to smooth the data.

RESULTS

In 1989, matrix potential (0-75 cm) under the stress (2.5 liters/vine/week) irrigation was less than the control at 93 DAP (August 23, 1989), 32 days after the stress irrigation treatment was implemented, and remained drier throughout the experiment (Fig. 1A). The greatest difference in matrix potential was found in the top 25 cm of soil (Fig. 1B). There were no differences in matrix potential at the lower soil depths (Fig. 1C, 1D).

Above Ground Vine Morphology 1989. Water-stressed vines showed a reduction of shoot growth (measured with meter stick) beginning 102 DAP (41 days after the water stress treatment was imposed) (Fig. 2A). This difference in relative shoot growth continued throughout the growing season. Water-stressed vines produced fewer number of mature nodes, persistent laterals, nodes on laterals, non-persistent laterals, and less dry leaf weight (DLW) compared to the control irrigated vines (Table 2). There were no yield, berry weight or berry size differences among control irrigated and stress irrigated vines. The control irrigated vines produced berries that had higher percent soluble solids than the water stressed-vines (Table 2).

Rootstock influenced shoot growth at all dates recorded (Fig. 2B). The own-rooted vines were the most vigorous. The 5BB vines, and Seyval/Seyval (S/S) vines had less terminal shoot growth compared to own-rooted vines 102 DAP (September 1, 1989) (Fig. 2B). There were rootstock effects on the number of mature nodes, number of nodes on laterals, and DLW (Table 2).

Fruited vines produced less shoot growth compared to defruited vines over the

entire growing season (Fig. 2C). Fruited vines produced fewer number of mature nodes, persistent laterals, nodes on persistent laterals, non-persistent laterals, and less dry leaf weight compared to defruited vines (Table 2). There were no differences in vine yield or cluster number among fruited vines. Cluster weight for water stressed and control irrigated vines was 310.4 and 320.0 g, respectively (data not shown). There were no differences in berry size or weight.

Below Ground Morphology 1989. Water stress, rootstock and crop load produced main effects and interactions for total fine root numbers at different depths (Table 3). Total root numbers (0-80 cm) were first counted from minirhizotron images at 64 DAP (July 25, 1989) (Fig. 3). There were no differences for total root numbers between the water stress and control treatments at any depth (Table 3).

There was a difference in total fine root numbers among the root systems at 64 DAP (July 25, 1989) (Table 3). By 85 DAP (August 15, 1989) this difference was no longer observed. At shallow depths (0 - 40 cm), there was a rootstock effect (Fig. 4A, Table 3). The S/S vines produced the greatest fine root numbers throughout most of the growing season (Fig. 4A). There was a difference in fine root numbers between S/S and 5BB (Fig. 4A), but there were no differences in fine root numbers between the 5BB and OR vines (Fig. 4A). There were no differences for total fine root numbers among the three root systems at deep (40 - 80 cm) depths (Table 3).

There were different crop load effects on total fine root numbers beginning at 114 DAP (Table 3). Fruited vines produced fewer fine roots than defruited vines (Fig. 3C). There were different crop load effects on shallow (0-40 cm) fine root numbers at 100

days after planting (Table 3). Fruited vines produced fewer shallow fine roots than defruited vines (Fig. 4B). Crop stress appeared to have no difference on root numbers at the 40 - 80 cm region of the soil (Table 3).

Total fine root numbers were influenced by water*crop interactions for total fine roots beginning at 114 DAP (Fig. 5, Table 3). Fruited vines grown under control irrigation produced more fine roots total than fruited vines under water-stress (Fig. 5). There were rootstock*crop interactions for shallow fine roots at 162 and 176 DAP (Fig. 6B, Table 3). The fruited S/S rootstock responded differently than when it was defruited (Fig. 6B). The other rootstocks (5BB and OR) responded similarly, regardless of whether or not the vine was fruited or defruited (Fig. 6A and C, respectively). There were water*crop interactions for deep fine roots beginning from 114 (September 13, 1989) to 176 DAP (November 14, 1989) (Fig. 4C, Table 3). Fruited vines grown under control irrigation produced more fine roots than fruited vines grown under stress-irrigation (Fig. 4C).

Second Year Results. In 1990, matrix potential (0-75 cm) under the stress irrigated plots (2.5 liters/vine/week; reduced to 1.8 liters/vine/week) was less than the control irrigated plots at 453 DAP (August 18, 1990), 24 days after the stress irrigation treatment was implemented and the soil remained drier throughout the experiment (Fig. 7A).

Above Ground Morphology, 1990. The greatest difference in matrix potential was in the top 25 cm of soil (Fig. 7B), but there were matrix potential differences at the 50 (Fig. 7C) and 75 cm soil depths (Fig. 7D). Drying occurred later as depth increased.

At 50 and 75 cm soil-depth, stress irrigated plots were drier than control irrigated plots from 450 to 525 DAP (August 18 to October 29, 1990) (Fig. 7C and D.).

Water stressed vines produced shorter shoots (411 DAP; August 11, 1990) and by the end of the growing season, water-stress reduced shoot length by 13% as compared to control-irrigated vines (Fig. 8A). From the middle of July to the middle of August there were no treatment differences in shoot length between the two irrigation treatment vines (Fig 8A). Water-stressed vines also produced less trunk dry weight as compared to control-irrigation vines (Table 4). There were no yield differences among the vines on the different irrigation treatments due to the inability of many of the vines stressed in year-1 to produce fruit in year-2. Control irrigated vines had lower percent soluble solids than the water stressed vines (Table 4). Control irrigated vines produced nearly twice the number of leaves as stressed vines (92 vs. 49, respectively). Stressed vines produced only 83% of the total leaf dry weight of control vines.

There was a rootstock effect on shoot growth during the middle of summer, but the difference subsided at the end of the growing season (Fig. 8B). There were no differences among rootstocks before of after these dates. Fruited vines produced less shoot growth compared to shoots of defruited vines at all recorded dates (Fig. 8C). Fruited vines produced fewer mature nodes and less dry weight of one-year-old shoots, two-year-old canes, and trunks (Table 4). There were no yield or cluster number differences among fruited vines. Total cluster weight of year-2 vines that were water stressed was unobtainable because only two vines produced crop. Control irrigated vines produced more clusters than the water stressed vines, but again, there were too many

missing values to determine crop load effects or berry size and weight values. Fruited vines produced 30% fewer leaves than defruited vines (58 vs. 82 leaves, respectively), and only 64% of the total leaf dry weight (g) (75 vs. 116 g., respectively).

Below Ground Morphology, 1990. Main effects of water stress, rootstock and crop load, and interactions affected total fine root count at different depths (Table 5). There were significant water stress effects on total fine root numbers across all depths (beginning at 453 DAP; August 18, 1990) (Table 5), at the shallow depths (beginning at 411 DAP; July 7, 1990) (Table 6), and at deep depths (beginning at 453 DAP; September 2, 1990) (Table 6). In each case, water stressed vines produced more fine roots than control-irrigated vines.

There were no significant rootstock main effects. There were significant crop load main effects. Vines with crop during year-one produced fewer total fine roots in year-two than did defruited vines (Fig. 9). The response was manifested earliest at the shallow depth (313 DAP; March 31, 1990) (Fig. 10B), and did occur later at deeper positions (341 DAP; April 28, 1990). In every case, defruited vines produced more fine roots than fruited vines (Fig. 11B). There was a water*crop (w*c) effect for total fine root numbers at 327 DAP; April 14, 1990) (Table 5). Water-stressed, defruited vines produced significantly more fine root numbers than water-stressed, fruited vines (data not shown). However, all control-irrigated vines produced a similar number of total fine roots, regardless of crop load (data not shown). There was a water*rootstock*crop load (w*r*c) effect at 411 to 468 DAP (July 7 to September 2, 1990) for total fine root numbers (Table 5). Water-stressed, fruited vines grafted to 5BB produced, on average,

9 times as many total fine roots than did vines of either S/S or OR category (40,460 total fine root numbers m^{-2} versus 5,375, and 5,247, respectively). From September 2 to the end of the growing season, water stressed, fruited vines on all rootstock categories produced similarly in regard to number of total fine roots (Table 5). There was also a water*rootstock*crop load (w*r*c) effect at 411 to 509 DAP (July 7 to October 13, 1990) for deep fine root numbers (Table 5, 6). Water-stressed, fruited vines grafted to 5BB produced more fine roots at the deep depth (beginning at 411 DAP; July 7, 1990) than did vines of either S/S or OR category. These two later categories produced more deep fine roots only on defruited vines (Table 6).

DISCUSSION

The objects of this study were to concomitantly determine water-stress, rootstock and crop load effects on above-and below-portions of Seyval vines. These data clearly showed that when excessive crop load was combined with inadequate soil-moisture, a poorly developed vine with low vigor and poor root and shoot system resulted, but root and shoot growth responded differently to water stress and crop load effects. Above-ground vegetative growth was inhibited by the water stress, whereas below-ground growth was stimulated by the water stress. Above-and below-ground morphology changed as matrix potential became more negative. Fine root activity increased with water stress but decreased with crop load. This root activity increase under water stress has been observed in grapevines (Smart and Coombe, 1983; Van Zyl, 1988), peaches, (Richards, 1976; Proebsting *et al.*, 1989), and field crops (Nonami and Boyer, 1990; Westgate and Boyer, 1985). These data suggest that root activity peaked and then

subsided over the growing season as a result of competition between vegetative and fruiting portions of the vine. Water stress caused a decrease in shoot length of the vines in this study, as was observed by other researchers (Freeman and Smart, 1976; Smart and Coombe, 1983; Lakso, 1985; Hsiao and Jing, 1987). Smart and Coombe (1983) reported that grapevine shoot growth was most sensitive to water stress during the spring and early summer. In this study, a specific sensitivity during spring and early summer was not observed, but shoot growth was more sensitive to water stress during the 1989 versus the 1990 growing season. Most likely, the vines during the second year were more established and had a deeper root system, increasing the resistance to the water stress.

There were strong responses to the combination of crop load and water stress in regard to total leaf number for both years. When fruited vines were water-stressed, total leaf number per vine was reduced. Vine leaf growth was more sensitive than root growth to water stress. Total root number of Seyval grapevines was inhibited by the presence of fruit on water-stressed vines. The data suggest stimulated root production on water-stressed vines with removal of fruit. Thus, as soil-water became limiting in a young vineyard, defruiting alleviated much of the water-stress effects on the vines, allowing vines to overcome the water shortage successfully.

In 1990, the first peak of root growth occurred in mid May and the second peak occurred mid October, approximately seven weeks post-harvest. Freeman and Smart (1976) and Van Zyl (1988) also reported two distinct peaks of root activity: one at early spring, and the other at post-harvest. The first and second peaks were of similar

magnitude in 1989. In 1990, the first peak was much smaller than the second peak, which disagrees with Freeman and Smart (1976), but the small first peak may have resulted from a combination of water and crop load stress response from the previous years treatments. The bimodal periodicity for root growth may be due to competition for carbohydrates (see Chapter IV) by fine roots and shoots as found by Atkinson (1980). The recovery of the fruited vines receiving inadequate irrigation during the last half of the 1990 season was due, primarily, to an extremely light crop load during the current growing season.

Water stress did not cause an increase in grapevine berry must pH, but the stress-irrigated vines were not subjected to an irrigation reduction until the middle of summer, and irrigation (at a reduced level) was continued throughout the growing season. It is likely that the cool summer temperature was insufficient to increase berry must pH which has been reported by other researchers (McCarthy and Coombe, 1985). In this experiment, water stress reduced total berry soluble solids in 1989, but increased it in 1990. The water-stressed vines were probably too young to withstand the irrigation and crop load stress of the first year and was unable to produce sufficient carbohydrates (measured dry matter partitioning) to adequately support both above and below-ground plant tissues. However, in second year the water stress increased the soluble solid contents of the berries growing on the water-stressed vines. The vines were more established and had a less dense canopy compared to the control-irrigated vines (measured by total leaf count). The clusters on the water-stressed vines were well exposed to incoming sunlight compared to the berries on the control-irrigated vines.

Berries in shaded canopies have reduced compositional values based on lower reduced sugar accumulation (Koblet and Perret, 1982).

Rootstock may contribute directly influence the scion via water uptake (Striegler and Howell, 1991), cold hardiness (Howell, 1988), storage of carbohydrates (Richards, 1986), and nutrient uptake (Hanson and Perry, 1989). In addition, there may be indirect effects which modify vine growth and produce smaller or larger vines (Pongranz, 1983). Further, an indirect response to rootstock has been demonstrated for fruit composition and cold hardiness via internal vine shading in vigorous rootstocks (Striegler and Howell, 1991). In this study of Seyval, rootstock selection affected vine vigor, but had no effect on vine yield for either year. Natali (1985) reported that Sangiovese vines grafted rootstocks of different vigor (Kober 5BB, 140 Ruggeri and own rooted vines) responded differently in regards to transpiration. Vines grafted to 140 Ruggeri had a higher transpiration rate than either 5BB or own-rooted vines upon rehydration. In this study, rootstock appeared to be responsible for the tremendous growth of deep fine roots during the 1990 growing season. The water-stressed and fruited vines grafted on 5BB rootstock produced more fine roots throughout the growing season compared to all other rootstocks and water combinations. The vines grafted on 5BB rootstock demonstrated an increased vigor compared to S/S and OR vines. The vines were weakened by water stress and heavy crop load in 1989. In 1990, with a reduced crop load, the vines grafted on 5BB rootstock appeared to adjust much better to the water deficit by producing a tremendous amount of new fine roots compared to the S/S and OR vines.

In terms of inhibition of vine yield and vegetative growth by crop stress,

Balaubrahmanyam, (1978) reported that the crop may influence carbohydrate reserves in the vine, and even light crop loads reduced root growth. Similar results was found in this study, a reduction in root production with crop load was observed in the 1989 growing season, and a reduction in root growth due to crop load for the first half of the 1990 growing season. The crop load effects were strong throughout the 1989 season because the vines were young, and the crop load excessive for 2-year-old-vines. During 1990, many of the water-stressed vines were unable to produce a crop in 1990 and the control-irrigated vines produced slightly less than they produced the year before. This explains why the second year crop load effects are seen during the early part of the growing season only. The crop load effect was no linger strong enough to reduce fine root numbers throughout the growing season.

There were no differences in leaf area between fruited and defruited vines in the 1990 data (1989 leaf area was not taken), though Lakso (1985) reported that crop load accentuates leaf area reduction. However, defruited vines did produce many more leaves than the fruited vines. In this study, vine yield suppression and reduced leaf number in year-two was due, in part, to excessive crop combined with low soil-moisture during the first season.

The results agree with previous studies of root growth inhibition by crop load. Head (1969) reported that even a small crop load during 1963 (3.6 and 7.1 kg/tree) and 1964 (12.0 and 14.4 kg/tree) in 13-year-old Worcester Pearmain apple trees on MM.104 rootstock was enough to reduce the quantity of new white roots from July onwards compared to de-blossomed trees. He also observed that the light crops had less effect

on shoot growth than on root growth and that heavy cropping would affect root growth more severely. A crop load of six clusters/vine reduced the number of new fine roots more so than crop load reduced shoot length.

In 1989, new fine root production accelerated during the first week of June. Though total fine root number was not influenced by water-stress fruiting status was of significant influence. Onset of root activity in 1989 was later than expected, and may have been be the result of transplant shock. Spring root growth began approximately 10 weeks after budburst in 1990, observable fine roots were first observed at the end of March. It was the middle of April, however, before new white fine roots were discernable along the tubes.

In 1990, new fine root production accelerated during the first week in August, and the impact of the water stress on fine roots was clear; there were more fine roots on the water-stressed vines (Fig. 9A). This agrees with Freeman and Smart (1976) in their work on Shiraz grapevine roots. The 1990 results agrees with Freeman and Smart (1976), but the 1989 results do not. Perhaps transplanting shock retarded root development in 1989. In 1989, the first peak of root growth occurred the middle of September, while the second peak appeared in the middle of November (one month post harvest). Freedman and Smart (1975) suggested that there is water uptake by suberized and unsuberized grapevine roots. This may have been the case with this study because root production was first seen in August, and shoot growth by this time was well underway. If there were few new roots growing at this time, the majority of water uptake must have been done by suberized roots. By the end of October, shoot growth

had ceased. In 1990, however, the shoot growth continued past veraison, an indication that the crop load effect was not severe enough to influence shoot growth. A rapid development of roots was observed during July of 1989 and May of 1990 in this study, but it was not determined whether the roots were new laterals or new primary roots.

Smucker (1990) commented on the tedium and other difficulties associated with past root measurement methodologies. The minirhizotron system is not without tedium or difficulties itself. Even though the minirhizotron system has certain limitations, the benefits of the system in regards to portability and efficiency in the field were acceptable. Sample size is an important factor to consider due to the high coefficient of variation associated with root sampling (Atkinson, 1980; McMichael *et al.*, 1987; Head, 1967; Atkinson, 1985). Size constraints of these plots in the rain exclusion shelter precluded other tube insertions, but for another such experiment with vines, additional tubes be inserted at either side of the vine, parallel to the rows at a distance of 30 cm. Increasing the number of observations per vine and compensating for the high variability associated with the minirhizotron system.

The Kalamazoo soil of our test site is a stratified soil, possibly making water (from a perched water table) available to deeper fine roots growing under inadequate irrigation. Spatial variety of soil horizons, soil texture and pore geometry are a few of the environmental factors that directly influence the patterns of root development and turnover (Smucker, 1990). Fine roots from water stressed vines in this experiment may have extracted water from lower, moister soil depths than the maximum 80 cm depth recorded. If so, the water stressed vines did not indicate as severe a response to the

irrigation treatments as may have been accomplished with a more precise containerized root study.

CONCLUSIONS

1. A heavy crop load reduced shoot length past veraison in 1989; a low crop load did not reduce shoot length past veraison in 1990 in Seyval vines.
2. Own-rooted Seyval vines produced more vigorous shoots during the 1989, but not during the 1990 growing season compared to vines grafted on 5BB or Seyval rootstocks.
3. Under conditions of water stress: fruit growth was favored over fine root growth, but root growth was favored over shoot and leaf growth in 1989; fine root growth was favored over fruit, shoot and leaf growth in 1990.
4. In 1989 and 1990, crop loading reduced total fine root numbers, while shoot length was reduced by both crop load and water stress.
5. The 1989 and 1990 data derived from this study show striking agreement with data derived from other methods of root study. Therefore, minirhizotron techniques should be included among the various effective tools for non-destructive, *in situ* root measurement of grapevines.

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Table 1. Effects of 1989 and 1990 Irrigation, Rootstock and Crop Load on Leaf Water Potential (ψ_l) (MPa) of Seyval Grapevines.

	10/4/89 101 DAP	10/6/90 488 DAP	10/28/90 502 DAP
Irrigation			
Stress[x]	4.21	4.5	6.4
Control[y]	1.71	2.0	2.8
	***[z]	***	***
Rootstock			
5BB	3.06	3.2	4.7
S/S	2.81	3.3	4.7
OR	3.01	3.1	4.5
	N.S.	N.S.	N.S.
Crop Load			
0 cluster	2.80	3.2	4.7
6 cluster	3.12	3.3	4.6
	N.S.	N.S.	N.S.

[z] **, ***, NS Significant at P = 0.01, 0.001, or nonsignificant, respectively.
[y]1989 and 1990 irrigated 10 liters of water/plant/week.
[x]1989 irrigated 2.5 liters of water/plant/week. 1990 irrigated 2.5 liters of water/plant/week; on 8/22/90 irrigation was decreased to 1.8 liters of water/plant/week.

Table 2. Effects of 1989 Irrigation, Rootstock, and Crop Load on Vegetative Growth of Seyval

Treatment	Mature nodes 10/89	Persistent laterals 10/89	No. of nodes on laterals 10/89	Non-persistent laterals 10/89	Dry leaf weight (g) 11/89	Berry soluble solids
Irrigation						
Stress[a]	28	4	5	10	15	13.8
Control[b]	46	8	17	15	28	16.2
	***[c]	***	***	***	***	**
Rootstock						
5BB	38ab[d]	6	14a	11	17b	15.5
S/S	32b	6	8b	13	21ab	14.3
OR	41a	6	10ab	14	26a	15.2
	*	N.S.	*	N.S.	*	N.S.
Irrigation x Rootstock						
Stress	33	3	6	10	17b	14.1
5BB	24	3	4	10	13b	13.7
S/S	28	4	4	11	15b	13.7
OR						
Control	42	8	21	13	18b	16.9
5BB	40	8	13	16	30a	14.9
S/S	54	9	16	17	37a	16.7
OR	N.S.	N.S.	N.S.	N.S.	**	N.S.
Crop Load						
0 cluster	55	10	18	17	28	NA
6 cluster	19	2	3	8	15	NA
	***	***	***	***	***	

[a]Irrigated 2.5 liters of water/plant/week.

[b]Irrigated 10 liters of water/plant/week.

[c]*, **, ***, and NS indicate statistical significance at P = 0.05, 0.01, 0.001, and nonsignificant, respectively.

[d]Mean separation within columns using LSD test at P = 0.05

Table 3. Statistical significance of 1989 Irrigation, Rootstock, and Crop Load Effects on Total (10-80 cm), Shallow (10-40 cm), and Deep (50-80 cm) Fine Root Numbers.

Days after planting	Factors			Interactions			
	Water	Rootstock	Crop	W*R	W*C	R*C	W*R*C
Total (0-80 cm)							
64		**					*
85							
100							
114			**		**		
132			**		*		
162			***		*		
176			**		*		
Shallow (0-40 cm)							
64		**					*
85							
100		*	**				
114		*	***				
132		*	**				
162		**	***			**	
176		*	***			*	
Deep (40-80 cm)							
64							
85							
100							
114					**		
132					*		
162					**		
176					**		

Table 4. Effects of 1990 Irrigation, Rootstock and Crop Load on Above Ground Vegetative Growth of Seyval Grapevines.

	# Mature nodes on 1 yr. old shoots	# Nodes on 2 yr. old canes	Dry wt. of 1 yr. old shoots (g)	Dry wt. of 2 yr. old canes (g)	Dry wt. of trunk (g)	Berry soluble solids
Irrigation						
Stress[a]	69	11	95	20	28	19.8
Control[b]	76	12	94	25	88	16.7
	N.S.	N.S.	N.S.	N.S.	*	***
Rootstock						
5BB	76	14	112a[d]	25	37	18.7
S/S	66	10	78b	23	34	18.2
OR	74	10	94ab	20	28	17.9
	N.S.	N.S.	***	N.S.	N.S.	N.S.
Crop Load						
0 cluster	78	13	114	29	35	NA
6 cluster	67	9	75	16	81	NA
	*[c]	N.S.	***	*	*	

[d] Mean separation within columns using LSD test at P = 0.05

[c] *, **, and NS indicate statistical significance at P = 0.05, 0.001, and nonsignificant, respectively.

[b]Irrigated 10 liters of water/plant/week.

[a]Irrigated 2.5 liters of water/plant/week.

Table 5. Statistical significance of 1990 Irrigation, Rootstock, and Crop Load Effects on Total (0-80 cm), Shallow (0-40 cm), and Deep (40-80 cm) Fine Root Numbers.

Days after planting	Factors			Interactions			
	Water	Rootstock	Crop	W*R	W*C	R*C	W*R*C
Total (0-80 cm)							
313			*				
327			*		**		
341			*				
356			*				
370			*				
383			*				
411							**
453	**						**
468	**						*
482	*						
496	**						
509	**						
Shallow (0-40 cm)							
313	**		**				
327			**				
341							
356			**				
370			*				
383							
411	*						**
453	**		*				
468	*		**				
482	**						
496	***						
509	*						
Deep (40-80 cm)							
313							
327							
341			*				
356			**				
370			**				
383			*				
411							*
453	**					**	***
468	**						***
482					*		
496	*						*
509	**						**

Table 6. Effects of 1990 Interaction of Water*Rootstock*Crop Load (w*r*c) on Numbers of Deep Roots (50-80 cm) of Seyval Grapevines.

	DAP[w]					
	411	453	468	482	496	509
Irrigation x Rootstock x Crop Load						
Stress[x], Seyval/5BB						
Stress, Seyval/Seyval						
defruited	11728	16590	18596	13657	15895	19599
fruited	0	2238	7870	11806	9954	7253
Stress, Seyval/Own Root						
defruited	8719	11960	13426	11882	15895	16744
fruited	0	1698	2701	6173	5864	4398
Control[y], Seyval/5BB						
defruited	2237	5324	4707	5401	4861	3627
fruited	1157	1736	1833	3762	2701	1543
Control, Seyval/Seyval						
defruited	1774	1158	1775	3009	2701	1775
fruited	2797	6173	8584	4147	7330	6173
Control, Seyval Own Root						
defruited	4244	8333	9414	10185	10185	9491
fruited	3318	7562	9259	15123	13272	12500
$LSD_{0.05z}$	6596	7341	8667	9036	9591	10397

[w]Irrigated 10 liters of water/plant/week.
[x]Irrigated 2.5 liters of water/plant/week; at 8/22/90 stress-irrigation was reduced to 1.8 liters of water/plant/week.
[y]Days after planting.

CAPTIONS FOR FIGURES

Figure 1. The 1989 matrix potential (MPa) of a Kalamazoo type soil (fine-loamy, mixed mesic Typic Hapludolfs) under a rain-exclusion shelter in Michigan. The letters "WS" represent the date of implementing the water stress treatment (July 22, 1989). (A) Overall 25-75 cm depth of matrix potential of stress (2.5 liters of water per plant per week) and control (10 liters of water per plant per week) irrigated 2- year-old Seyval grapevines. (B) Matrix potential at 25 cm depth, (C) Matrix potential at 50 cm depth, (D) Matrix potential at 75 cm depth. Each value represents the mean of five replications. Vertical lines represent SE.

Figure 2. The 1989 effects of irrigation, rootstock and crop load on shoot length in Seyval grapevines. The letters "ws", "v", and "h" refer to the dates of (implementing) the water stress treatment (July 22, 1989), veraison (August 18, 1989), and fruit harvest (September 28, 1989), respectively. (A) irrigation, each value represents the mean of 30 vines, (B) rootstock, each value represents the mean of 20 vines, and (C) crop load, each value represents the mean of 30 vines. Vertical lines represent SE.

Figure 3. The 1989 effects of crop load on total root number (0-80 cm) m^{-2} between defruited and fruited vines. The letters "ws", "v", "h", and "ld" refer to the dates of (implementing) the water stress treatment (July 22, 1989), veraison (August 18, 1989), fruit harvest (September 28, 1989), and leaf drop (October 9, 1989), respectively. Each value represents the mean of 30 vines. Vertical lines represent SE.

Figure 4. The 1989 effects of rootstock, crop load on shallow (0-40 cm), and the interaction of irrigation and crop load on deep (40-80 cm) root numbers m^{-2}. The letters "ws", "v", "h", and "ld" refer to the dates of (implementing) the water stress treatment (July 22, 1989), veraison (August 18, 1989), fruit harvest (September 28, 1989), and leaf drop (October 9, 1989), respectively. (A) Rootstock. Each value represents the mean of 20 vines. (B) Crop load. Each value represents the mean of 30 vines. (C) The interaction between irrigation (stress = 2.5 liters of water per plant per week, and control =10 liters of water per plant per week), and crop load (fruited and defruited vines). Each value represents the mean of 15 vines. Vertical lines represent SE.

Figure 5. The 1989 effects of the interaction between irrigation (stress = 2.5 liters of water per plant per week, and control = 10 liters of water per plant per week), and crop load (defruited = 0 clusters/vine, fruited = 6 clusters/vine) on total (0-80 cm) root numbers m^{-2}. The letters "ws", "v", "h", and "ld" refer to the dates of (implementing) the water stress treatment (July 22, 1989), veraison (August 18, 1989), fruit harvest (September 28, 1989), and leaf drop (October 9, 1989), respectively. Each value represents the means of 15 vines. Vertical lines

represent SE.

Figure 6. The 1989 effects of the interaction between crop load (defruited = 0 clusters/vine, fruited = 6 clusters/vine), and rootstock on shallow (0-40 cm) root numbers m^{-2}. (A) 5BB = Seyval grafted to 5BB rootstock. (B) S/S = Seyval grafted to Seyval rootstock. (C) OR = own rooted Seyval vines. The letters "ws", "v", "h", and "ld" refer to the dates of (implementing) the water stress treatment (July 22, 1989), veraison (August 18, 1989), fruit harvest (September 28, 1989), and leaf drop (October 9, 1989), respectively. Each value represents the mean of 10 vines. Vertical lines represent SE.

Figure 7. The 1990 matrix potential (MPa) of a Kalamazoo type soil (fine-loamy, mixed mesic Typic Hapludolfs) under a rain-exclusion shelter in Michigan. The letters "WS" represent the date of implementing the water stress treatment (July 22, 1990). (A) Overall 25-75 cm depth of matrix potential of stress (2.5 liters of water per plant per week) and control (10 liters of water per plant per week) irrigated 3-year-old Seyval grapevines. (B) matrix potential at 25 cm depth, (C) matrix potential at 50 cm depth, (D) matrix potential at 75 cm depth. Each value represents the mean of five replications. Vertical lines represent SE.

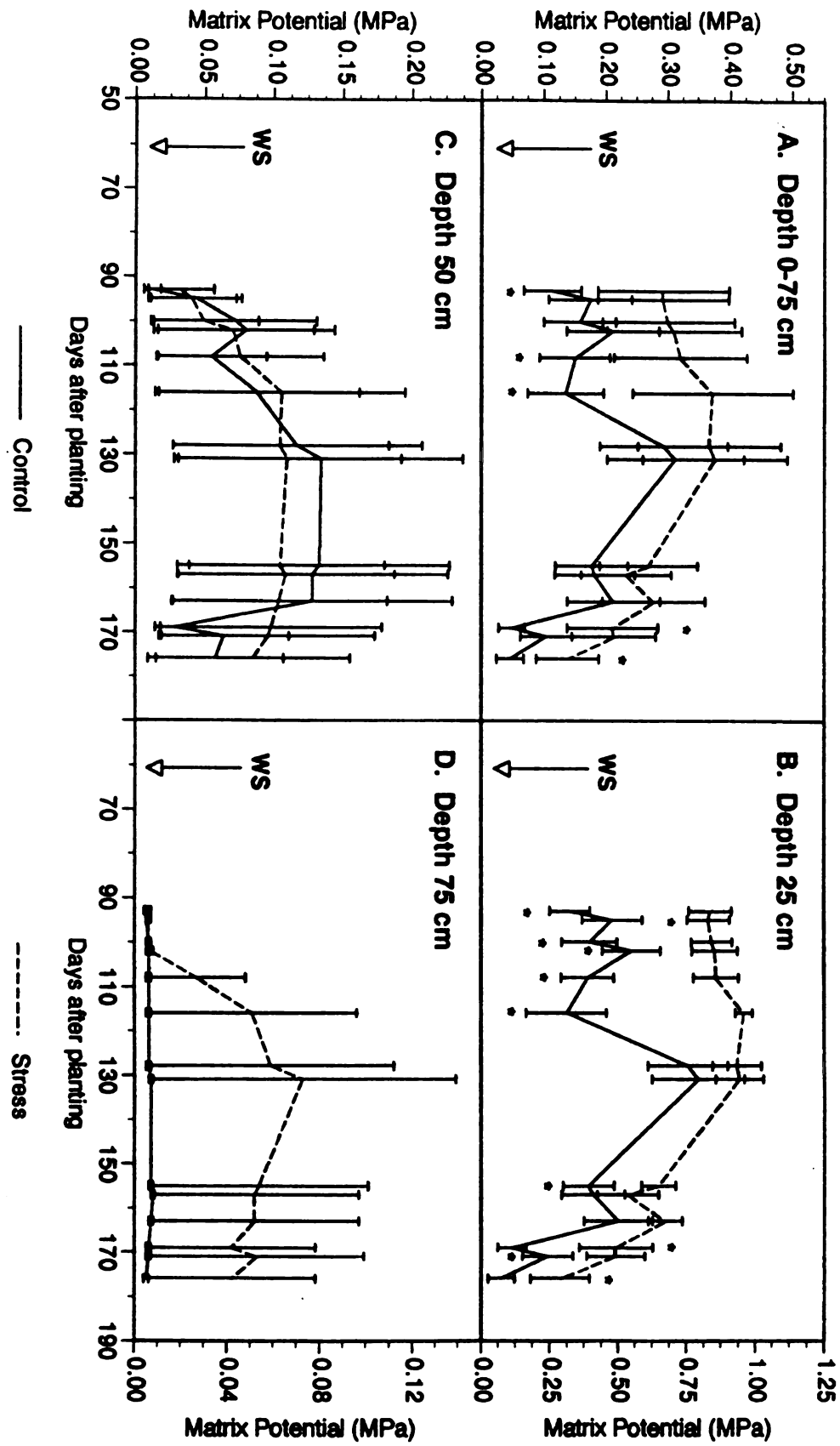
Figure 8. The 1990 effects of irrigation, rootstock and crop load on shoot length in Seyval grapevines (A) irrigation, each value represents the mean of 30 vines, (B) rootstock, each value represents the mean of 20 vines, and (C) crop load. The letters "bb", "b", "ws", "v", and "h" refer to the dates of bud burst (May 6, 1990), bloom (June 6, 1990), (implementing) the water stress treatment (July 22, 1990), veraison (August 22, 1990), and fruit harvest (September 21, 1990), respectively. Each value represents the mean of 30 vines. Vertical lines represent SE.

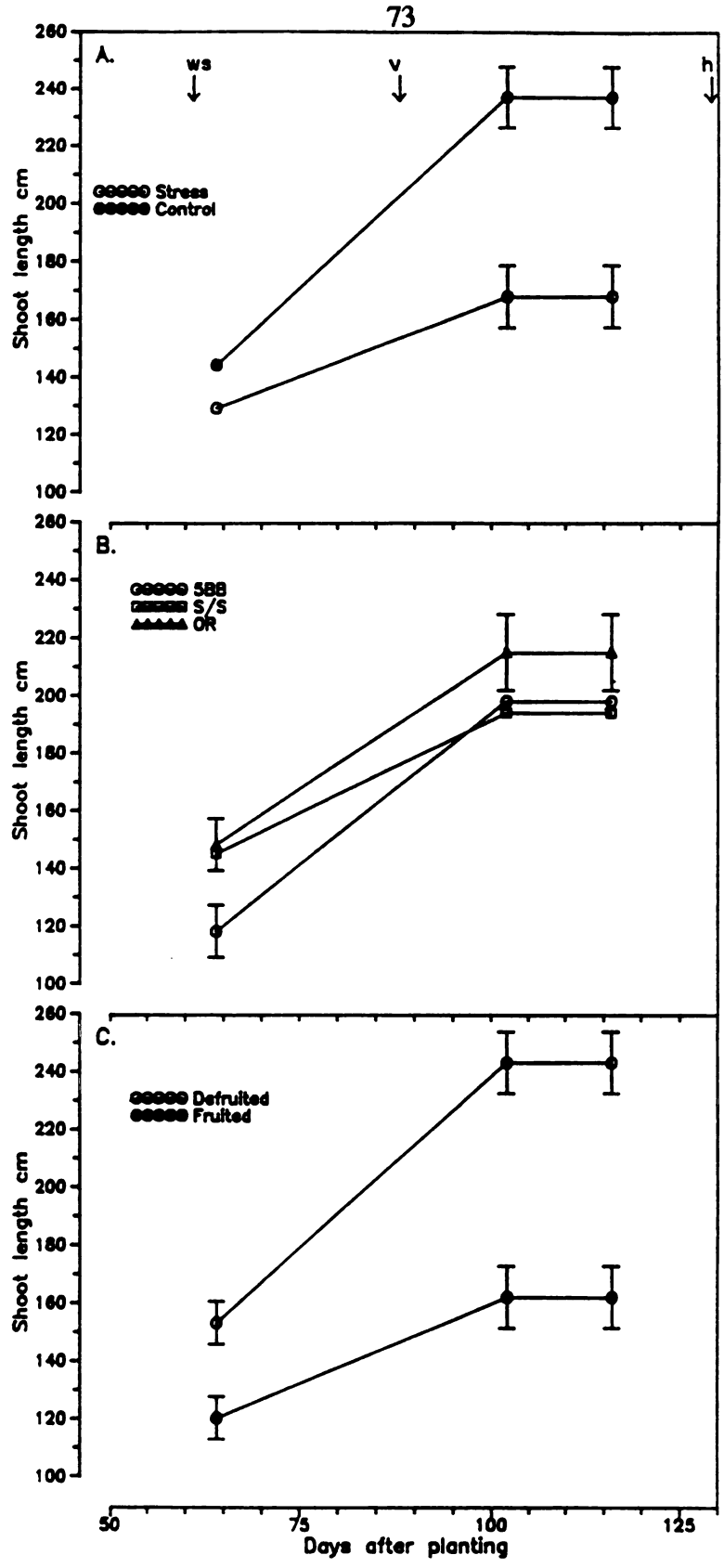
Figure 9. The 1990 effects of (A) irrigation (stress=2.5 liters of water per plant per week, later reduced to 1.8l/p/w on 8/22/90; control = 10 liters of water per plant per week), and (B) crop load (defruited = 0 clusters/vine, fruited = maximum of 6 clusters/vine) on total (0-80 cm) root numbers m^{-2}. The letters "bb", "b", "ws", "v", and "h" refer to the dates of bud burst (May 6, 1990), bloom (June 6, 1990), (implementing) the water stress treatment (July 22, 1990), veraison (August 22, 1990), and fruit harvest (September 21, 1990), respectively. Each value represents the mean of 30 vines. Vertical lines represent SE.

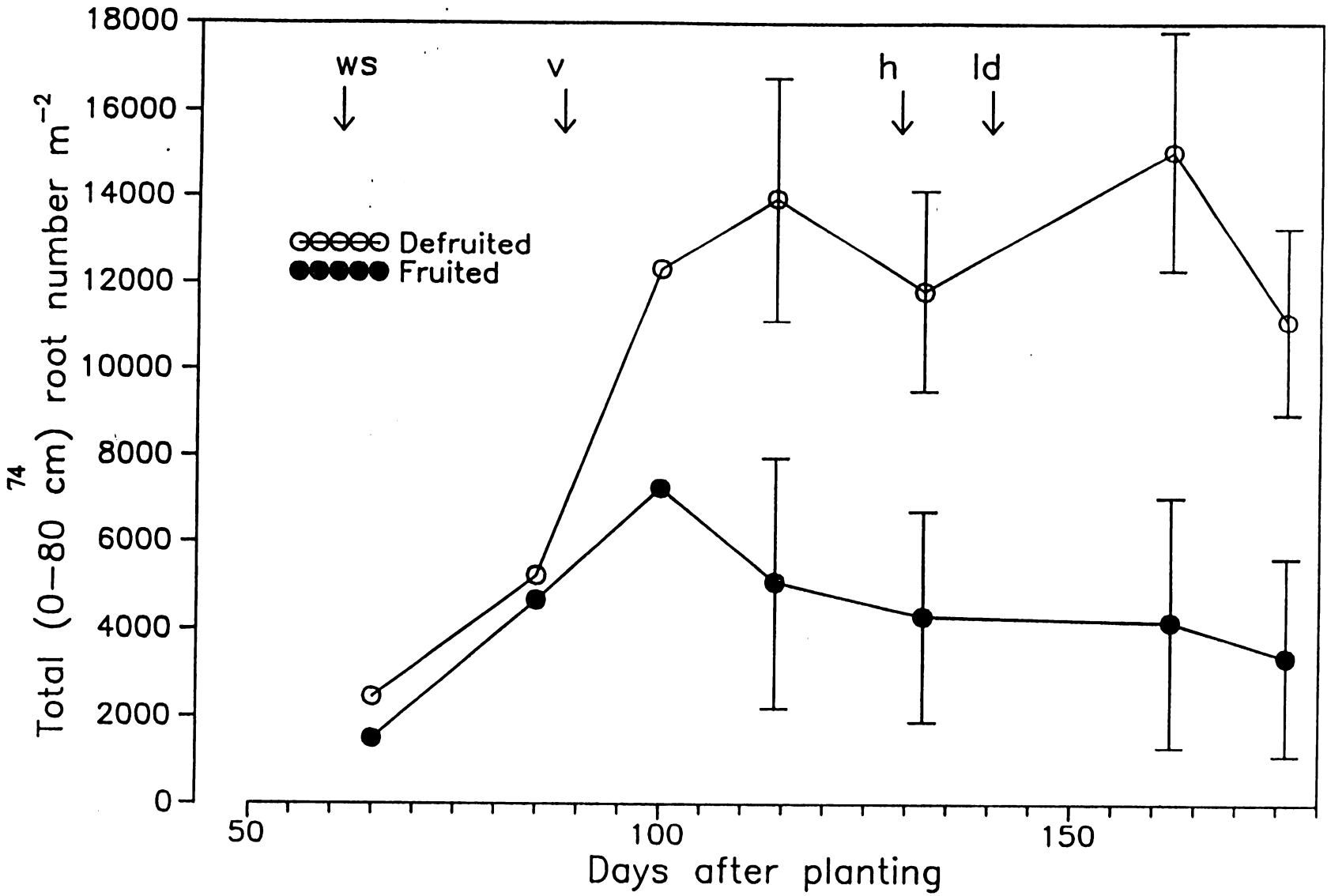
Figure 10. The 1990 effects of (A) irrigation (stress=2.5 liters of water per plant per week, later reduced to 1.8l/p/w on 8/22/90; control = 10 liters of water per plant per week), and (B) crop load (defruited = 0 clusters/vine, fruited = maximum of 6 clusters/vine) on shallow (0-40 cm) root numbers m^{-2}. The letters "bb", "b", "ws", "v", and "h" refer to the dates of bud burst (May 6, 1990), bloom (June 6, 1990), (implementing) the water stress treatment (July 22, 1990),

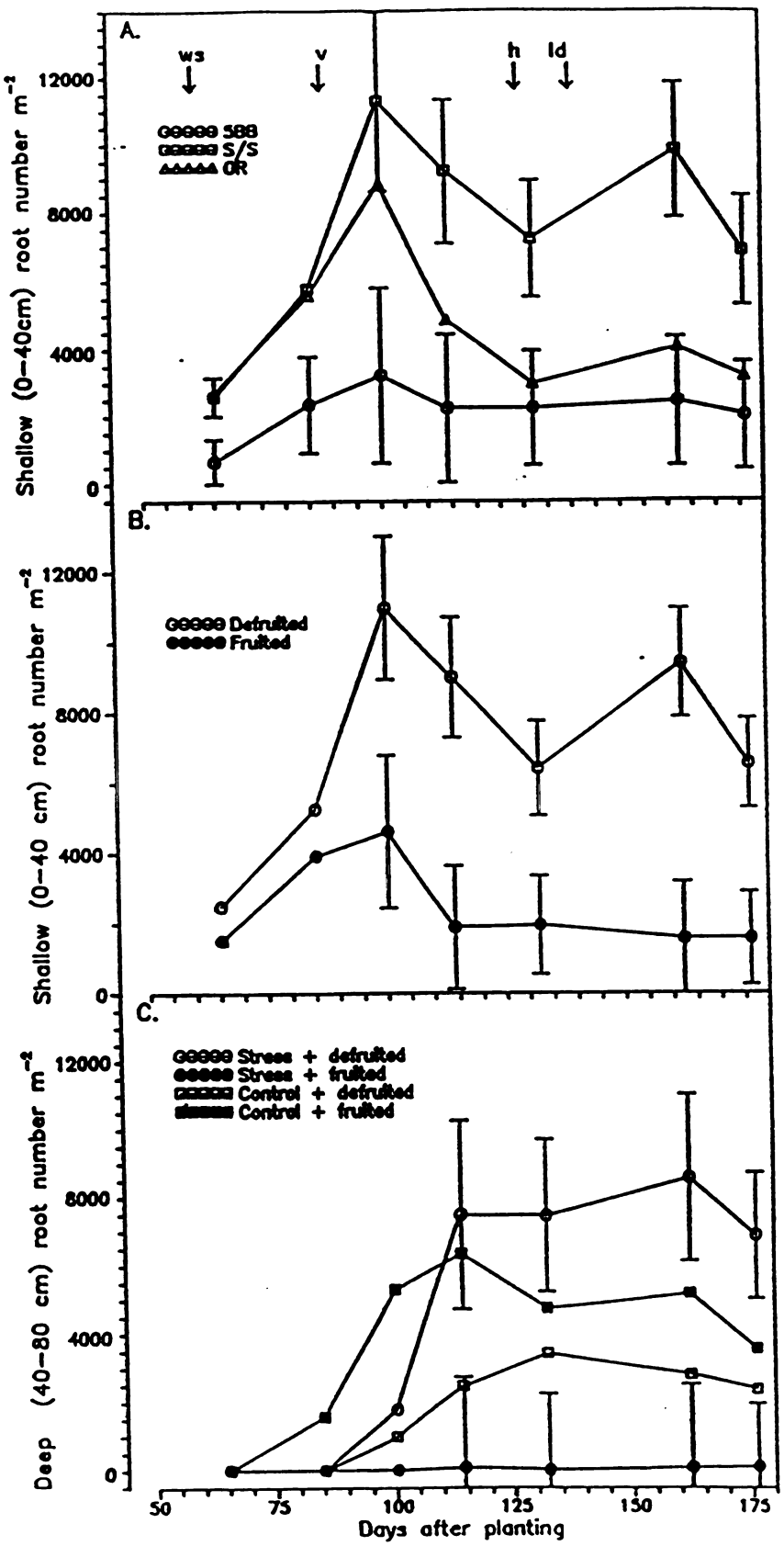
veraison (August 22, 1990), and fruit harvest (September 21, 1990), respectively. Each value represents the mean of 30 vines. Vertical lines represent SE.

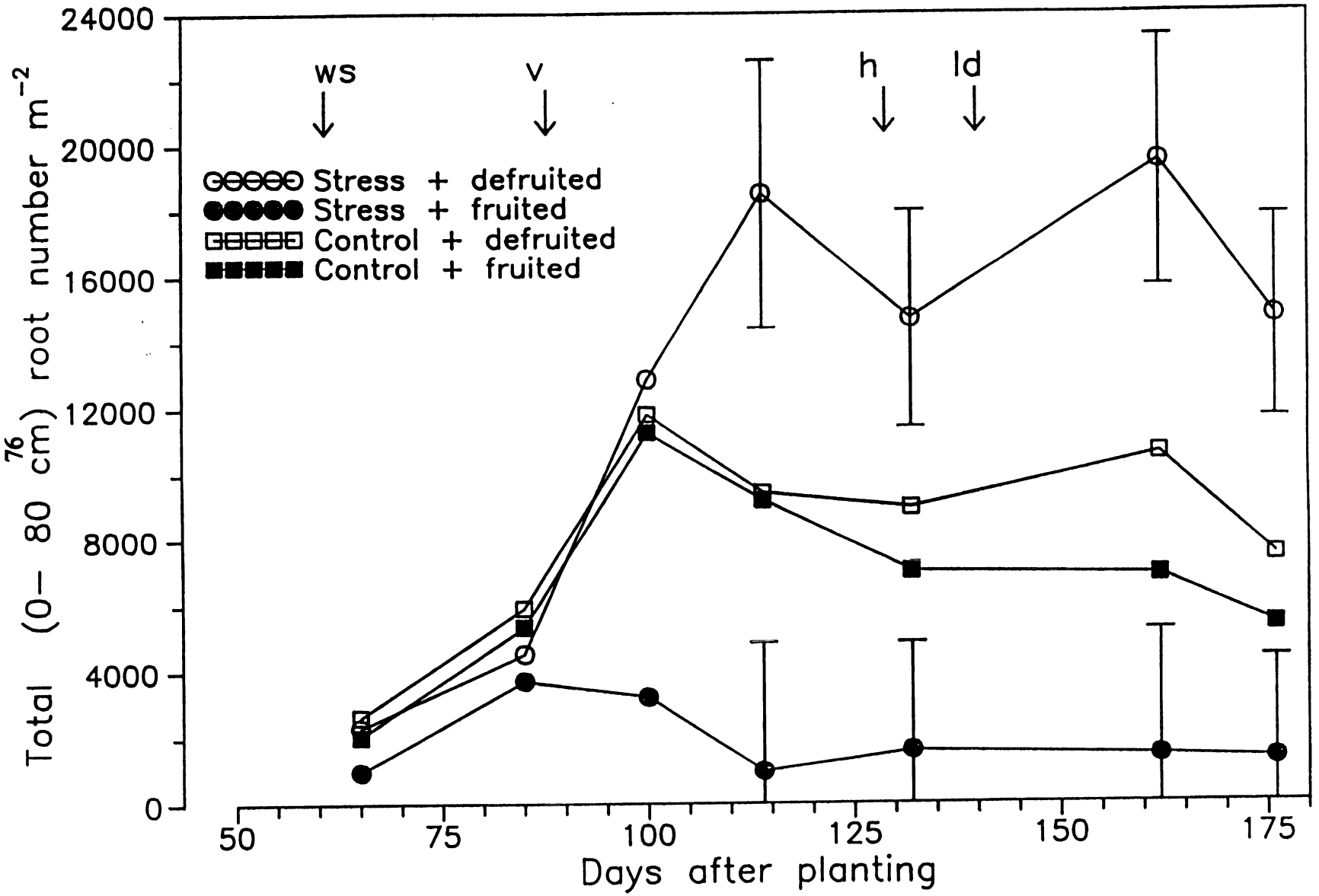
Figure 11. The 1990 effects of (A) irrigation (stress=2.5 liters of water per plant per week, later reduced to 1.8l/p/w on 8/22/90; control = 10 liters of water per plant per week), and (B) crop load (defruited = 0 clusters/vine, fruited = maximum of 6 clusters/vine) on deep (40-80 cm) root numbers m^{-2}. The letters "bb", "b", "ws", "v", and "h" refer to the dates of bud burst (May 6, 1990), bloom (June 6, 1990), (implementing) the water stress treatment (July 22, 1990), veraison (August 22, 1990), and fruit harvest (September 21, 1990), respectively. Each value represents the mean of 30 vines. Vertical lines represent SE.

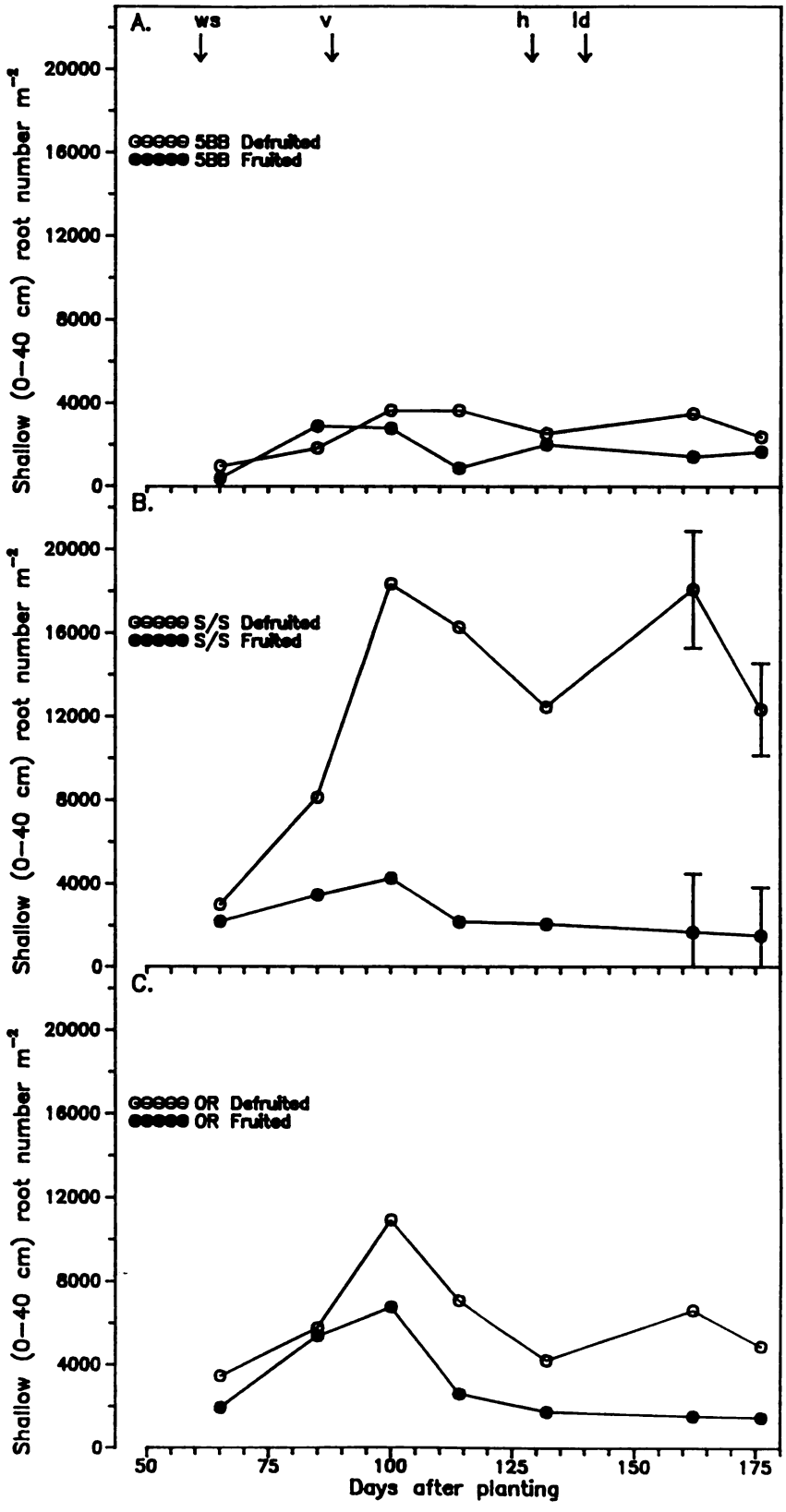

A. Depth 0-75 cm
B. Depth 25 cm
C. Depth 50 cm
D. Depth 75 cm
WS
Matrix Potential (MPa)
Days after planting
Control
Stress

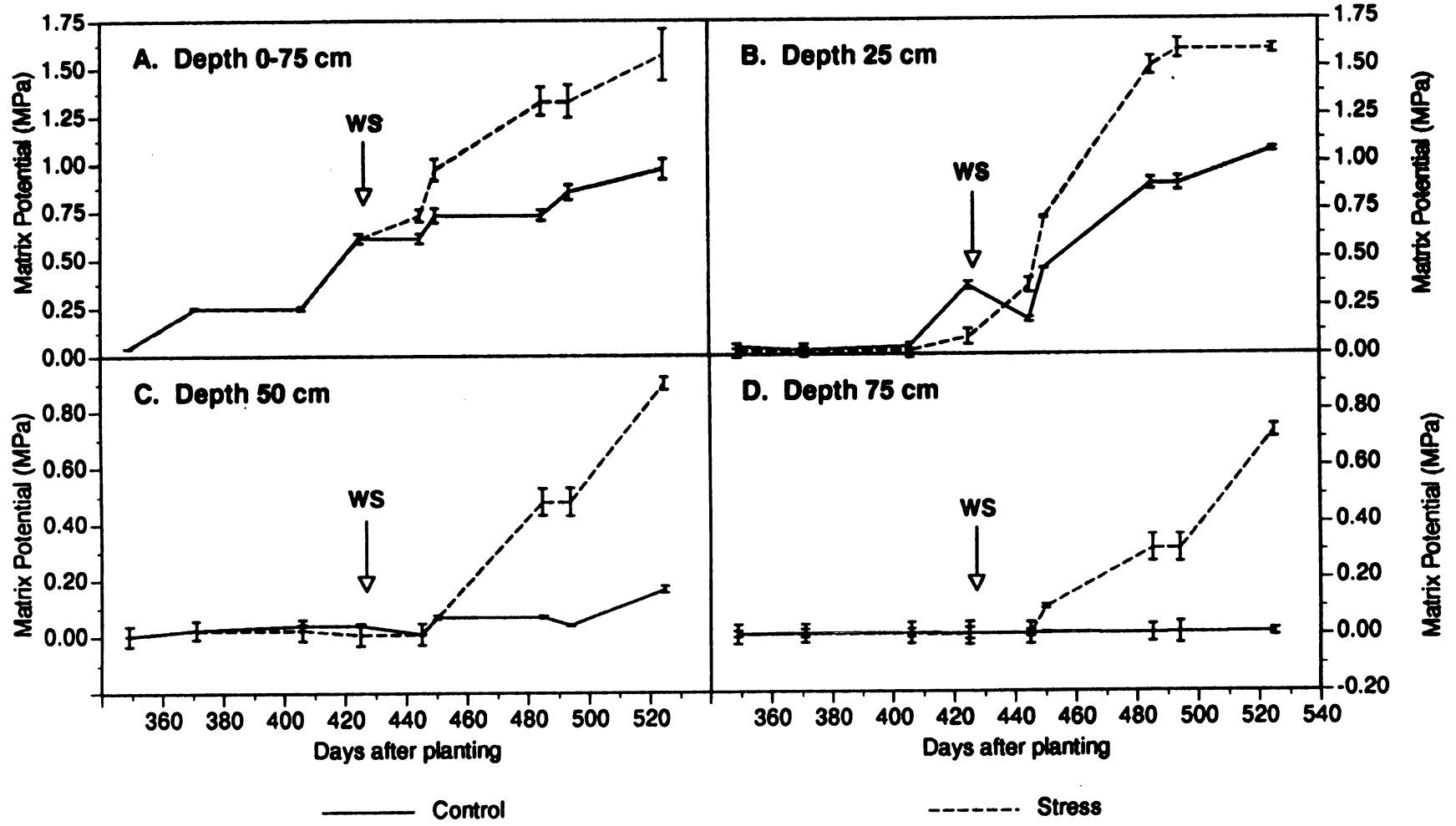

A.
ws
v
h
Stress
Control
B.
588
S/S
OR
C.
Defruited
Fruited
Shoot length cm
260
240
220
200
180
160
140
120
100
50
75
100
125
Days after planting

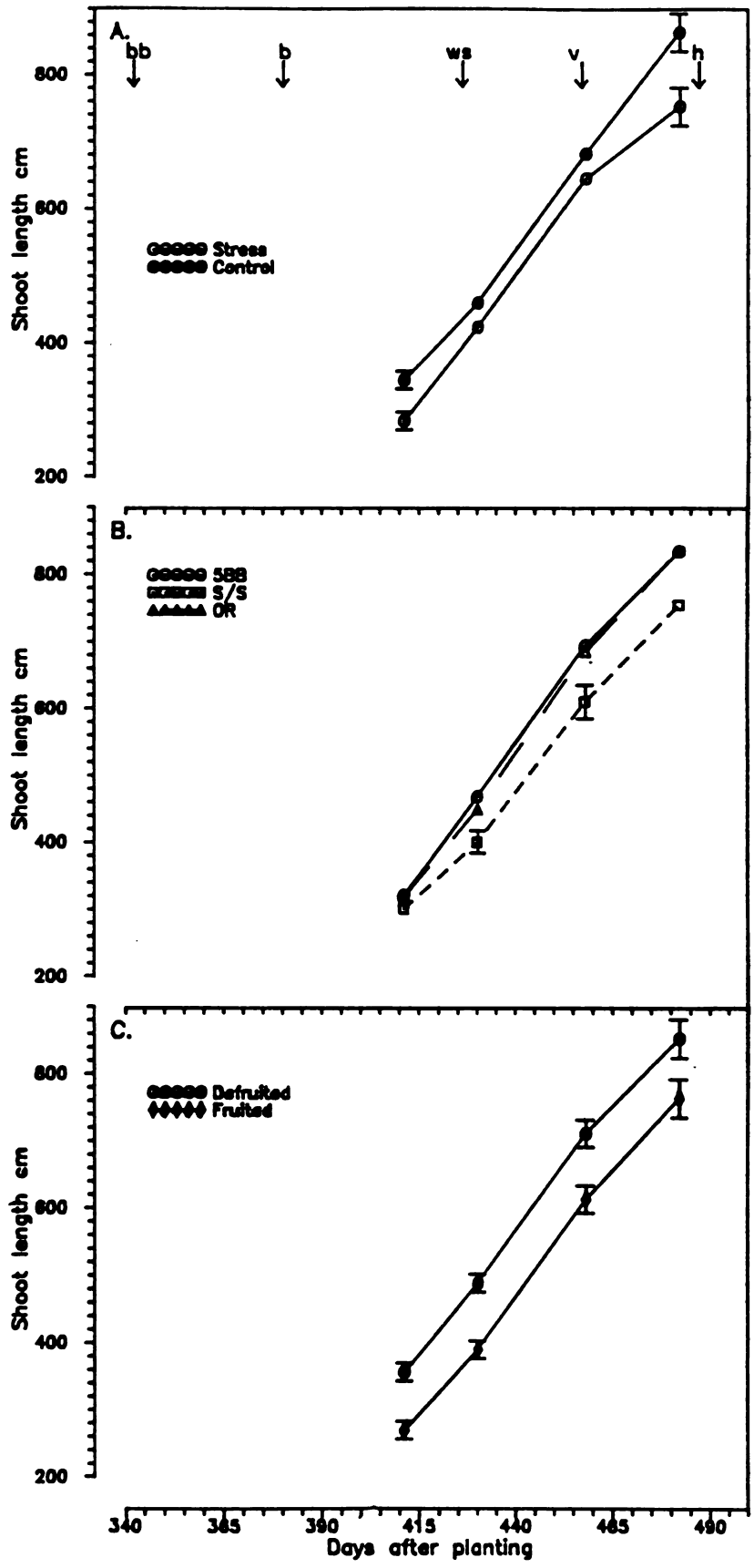

18000
16000
14000
12000
10000
8000
6000
4000
2000
0
Total (0–80 cm) root number m^{-2}
ws
v
h
ld
Defruited
Fruited
50
100
150
Days after planting

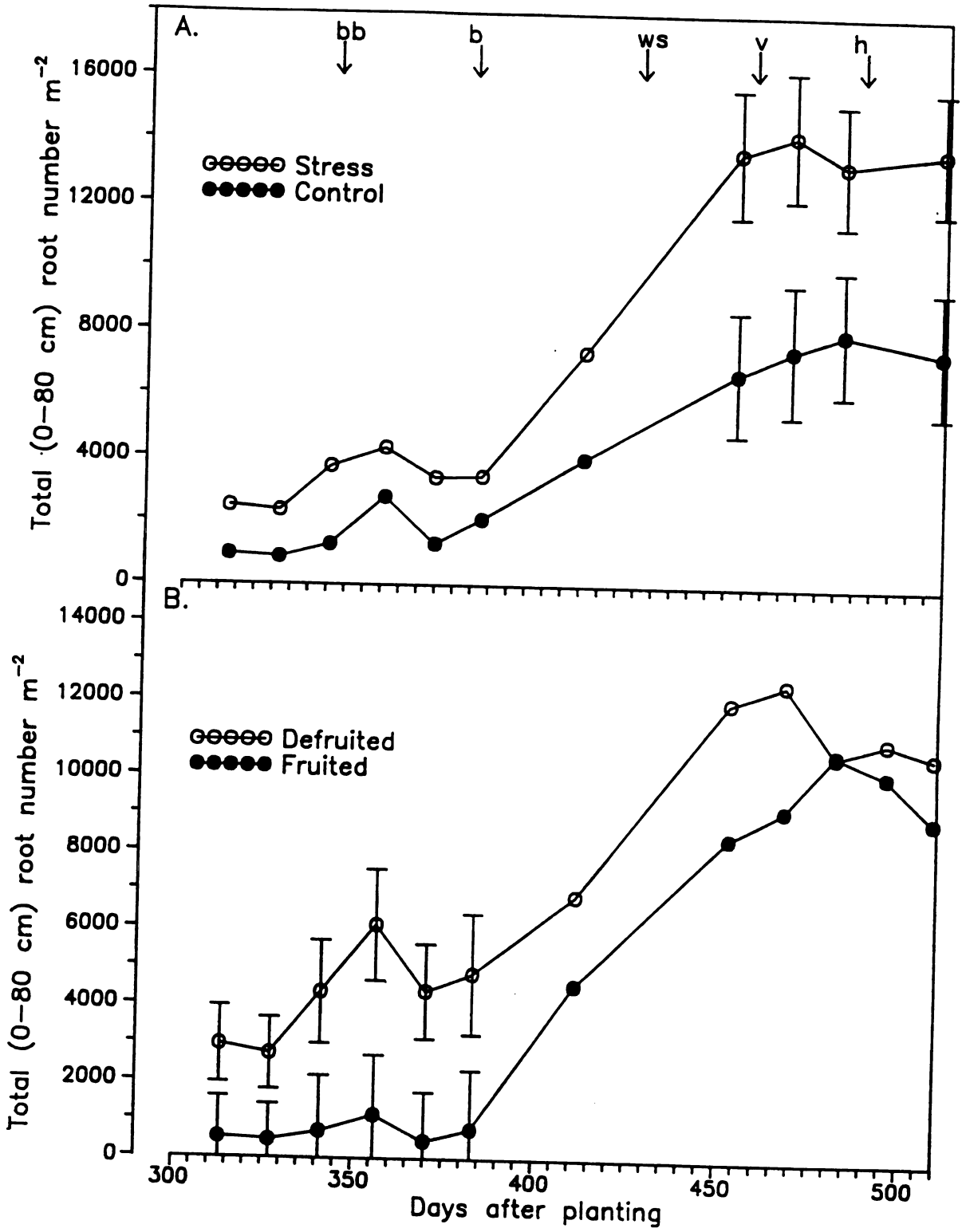

A.
ws
v
h
ld
588
S/S
OR
Shallow (0–40cm) root number m⁻²
12000
8000
4000
0
B.
Detrufted
Frufted
Shallow (0–40 cm) root number m⁻²
C.
Stress + detrufted
Stress + frufted
Control + detrufted
Control + frufted
Deep (40–80 cm) root number m⁻²
50
75
100
125
150
175
Days after planting

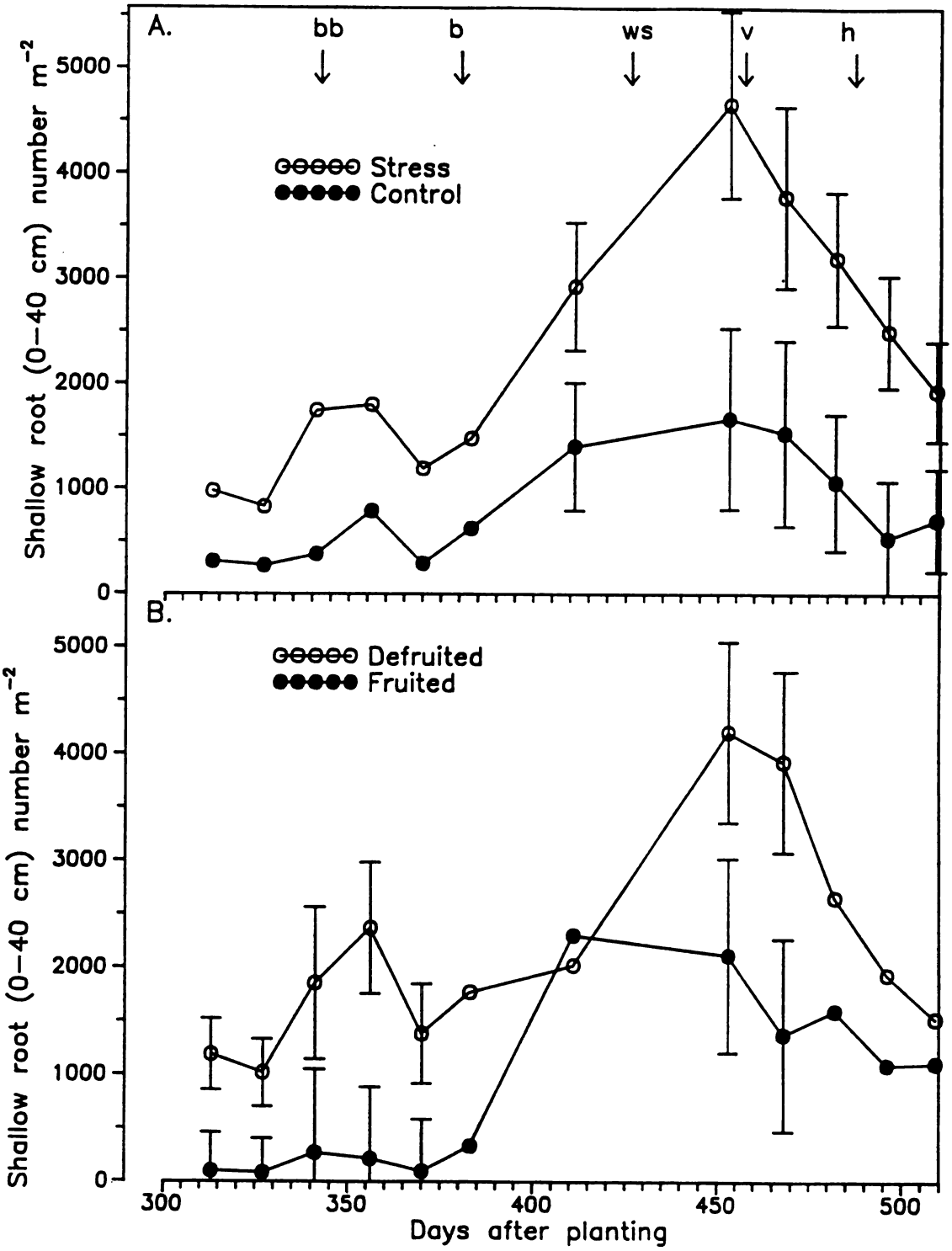

24000
20000
16000
12000
8000
4000
0
Total (0– 80 cm) root number m^{-2}
ws
v
h
ld
Stress + defruited
Stress + fruited
Control + defruited
Control + fruited
50
75
100
125
150
175
Days after planting

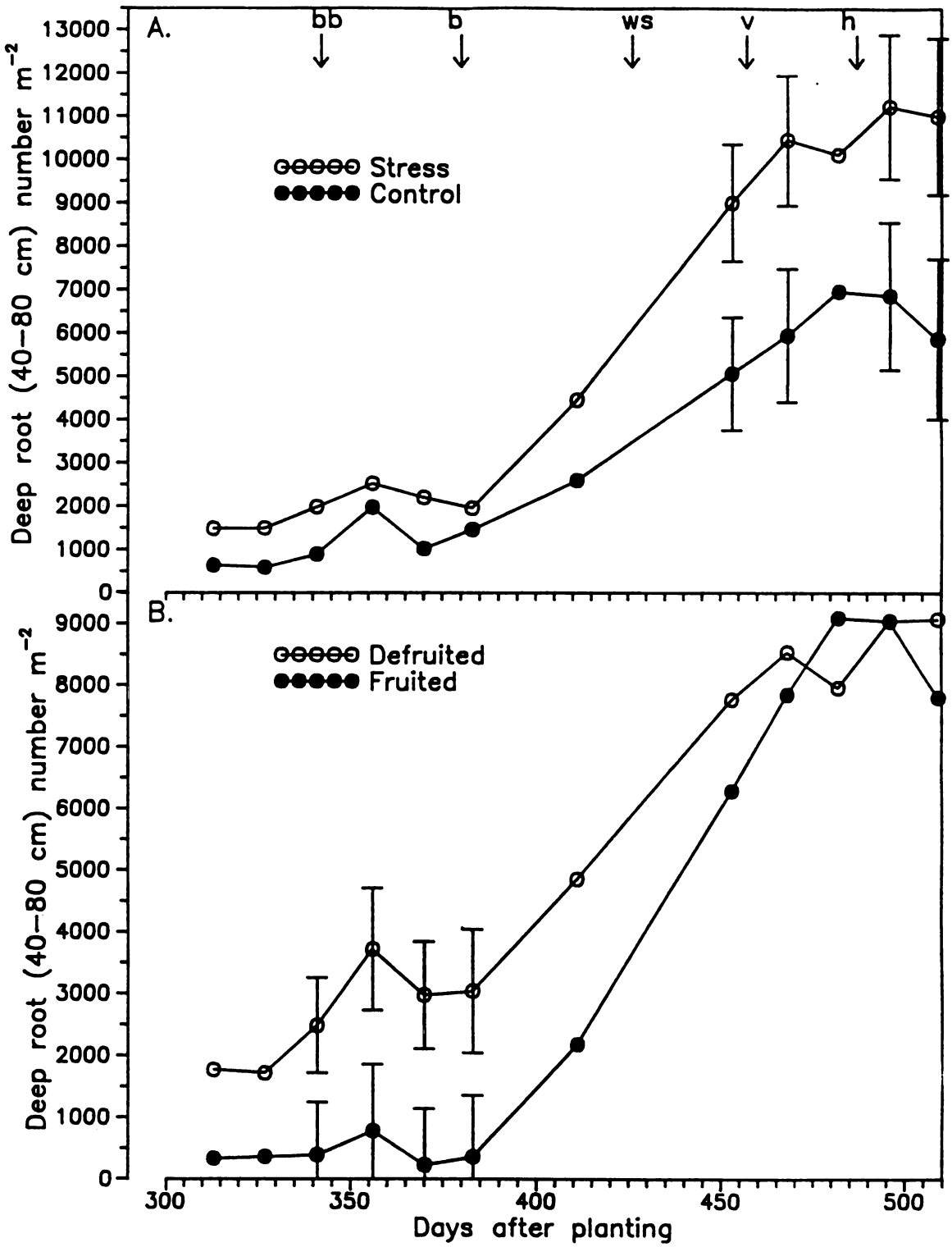

A.
ws
v
h
ld
5BB Defruited
5BB Fruited
B.
S/S Defruited
S/S Fruited
C.
OR Defruited
OR Fruited
Shallow (0-40 cm) root number m⁻²
0
4000
8000
12000
16000
20000
50
75
100
125
150
175
Days after planting


A. Depth 0-75 cm
B. Depth 25 cm
C. Depth 50 cm
D. Depth 75 cm
WS
Matrix Potential (MPa)
Days after planting
Control
Stress


A.
bb
b
ws
v
h
Stress
Control
B.
SBB
S/S
OR
C.
Defruited
Fruited
Shoot length cm
200
400
600
800
340
365
390
415
440
465
490
Days after planting


A.
bb
b
ws
v
h
Stress
Control
Total (0–80 cm) root number m^{-2}
16000
12000
8000
4000
0
B.
Defruited
Fruited
14000
12000
10000
8000
6000
4000
2000
0
300
350
400
450
500
Days after planting


A.
bb
b
ws
v
h
Stress
Control
Shallow root (0–40 cm) number m^{-2}
5000
4000
3000
2000
1000
0
B.
Defruited
Fruited
Shallow root (0–40 cm) number m^{-2}
5000
4000
3000
2000
1000
0
300
350
400
450
500
Days after planting


A.
bb
b
ws
v
h
Stress
Control
Deep root (40–80 cm) number m^{-2}
13000
12000
11000
10000
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
B.
Defruited
Fruited
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
300
350
400
450
500
Days after planting

CHAPTER IV: EFFECTS OF CROP LOAD AND LOW SOIL-WATER CONDITIONS ON GAS EXCHANGE AND CARBOHYDRATE PARTITIONING IN SEYVAL GRAPEVINES

ABSTRACT

Two-year old grapevines grafted to different root systems were exposed to water and crop load stress to determine carbohydrate partitioning and photosynthesis variables of single vine leaves: net $C0_2$ assimilation (A), stomatal conductance (g_s), transpiration (E), and water use efficiency (WUE). The interrelationships between water-stress, rootstocks, and crop stress with abscisic acid (ABA) content of grapevine leaves was also investigated. Two-year-old own-rooted and Seyval grafted to 5BB and to Seyval were grown under a rain exclusion shelter. Treatments were: 1) cropping level, either 0 or 6 clusters/vine, and 2) irrigation level, either 10 or 2.5 liters of water/plant/week. In general, g_s was affected more than A. Fruited vines had greater g_s, E, and lower WUE and dry leaf weight (DLW) compared to defruited vines. Vines grown under water-stress had lower A, g_s, E, and DLF, and higher WUE compared to vines grown under the control-irrigated level. ABA contents of water-stressed leaves were greater than leaves of control-irrigated vines.

KEY WORDS: rootstocks, soil-water deficit, abscisic acid, gas exchange

INTRODUCTION

Many environmental and physiological variables affect vine photosynthesis (Smart, 1974b; Hardie and Considine, 1976; Liu *et al.*, 1978). Among the physiological variables there includes stomatal conductance (g_s) (Sepulveda and Kliewer, 1986; During, 1987; Zhang *et al.*, 1987; Zhang and Davies, 1989, 1990), transpiration (E) (Gentry and Stout, 1971; Smart, 1974b), and abscisic acid (ABA) (Loveys and Kriedmann, 1974; During and Loveys, 1982; Nomami and Boyer, 1990). Environmental variables include water-stress ((Kriedmann and Smart, 1971; McCree and Richardson, 1987), rootstock (Bravdo, *et al.*, 1972; Smart and Coombe, 1983; Candolfi-Vasconcelos, 1993) and crop load (Hale and Weaver, 1962; Geiger, 1976; Kaps and Cahoon, 1989).

Water-Stress. Water-stress has a tremendous effect on grapevine photosynthesis (Kriedemann and Smart, 1971; McCree and Richardson, 1987), influencing the grapevine directly or indirectly. Direct influence may occur by impairing the photosynthetic apparatus of the vine and limiting the biological process, or it may occur indirectly, by regulating part of the photosynthetic apparatus, such as stomatal aperture, thus reducing the supply of CO_2 to the leaf (Kliewer *et al.*, 1984).

The stomata respond to CO_2 level, light quality and intensity, soil-moisture (Zhang and Davies, 1987), leaf water status, and leaf ABA levels (Farquhar and Sharkey, 1982), control CO_2 entry into the leaves while also preventing desiccation of the plant. At high water-stress, the stomata probably are responsible for reducing photosynthesis (Kriedemann and Smart, 1971).

Rootstock Effects. It is well established that grapevine drought tolerance (Pongracz, 1983; Carbonneau, 1985) and productivity (vegetative and reproductive) are influenced

by the rootstock (Pongracz, 1983; Striegler and Howell, 1991; Swanepoel and Southey, 1989; McCarthy and Cirami, 1990; Koblet *et al.*, 1993). Rootstock also influences photosynthesis by increasing vine vigor and E in rooted cuttings of grapevines (Bravdo *et al.*, 1972; Smart and Coombe, 1983). Bravdo *et al.* (1972) working with *V. vinifera* vines indicated that more vigorous cultivars (Thompson seedless and Perlette) had greater leaf area and number, which increased water use efficiency (WUE) and photosynthesis compared to less vigorous cultivars (Pearl of Csaba).

Crop Load Effects. Fruit load has been reported to affect photosynthesis in many crops including peach (Dejong, 1986), tomatoes (Gucci and Flore, 1989), apples (Hansen, 1967, Avery, 1977), sour cherry (Flore and Sams, 1986), and grapevines (Geiger, 1976; Gutierrez *et al.*, 1985; Downton *et al.*, 1987; Chavez, 1989; Kaps and Cahoon, 1989). However, the crop load effect on photosynthesis is not clear. Geiger (1976) reported mixed results with crop load: promoting, inhibiting, or having no effect on photosynthesis. Other researchers found no crop load effect on photosynthesis in apple (Rom and Ferree, 1986), sweet cherry (Roper *et al.*, 1988), and grapevines (Williams and Smith, 1985). Generally, the fruit crop is a strong sink (Hale and Weaver, 1962; Richards, 1986), but the photosynthetic response can vary with cultivar (Avery, 1977; Barden, 1971), rootstock (Barden, 1971), leaf age (Kriedemann et al., 1970; Barden, 1971), diurnal changes (Geiger, 1976; Downton *et al.*, 1987), seasonality (Chaves, 1984; Flore and Sams, 1986), state of fruit maturity (Geiger, 1976; Gutierrez et al., 1985; Flore and Sams, 1986; Downton *et al.*, 1987; Gucci and Flore, 1989; Gutierrez *et al.*, 1985), as well as increased crop load (Kaps and Cahoon, 1989).

Abscisic acid (ABA) Effects. Abscisic acid can modify photosynthesis in grapevines. The concentration of ABA increases in many cultivars (Concord, Napa Gamay, and Carignane) when vines are exposed to water-stress (Loveys and Kriedemann, 1973). ABA levels increase during soil-drying cycles, and return to near-original pre-stress levels when the water potential is restored (Loveys and Kriedemann, 1973). There have been many reports that ABA content in leaves increases in water-stressed grapevines, but much less information is available on how rootstock and crop load affects the ABA content.

The main objective of this study was to evaluate the interactions between water stress, rootstock and crop load on carbohydrate partitioning and the gas exchange variables, CO_2 assimilation rate (A), g_s, E, and water use efficiency, (WUE), as well as leaf ABA of field grown Seyval (Seyve-Villard 5-276) grapevines grafted to root systems of differing vigor. Also, responses of newly planted vines (1989) was compared to the same vines the following year when they were well established (1990).

MATERIALS AND METHODS

Location and Soils. This experiment was conducted at the Kellogg Biological Station, Battle Creek, Michigan, on a Kalamazoo type soil (fine-loamy, mixed mesic Typic Hapludolfs) located in an automated rain-exclusion shelter (Martin *et al.*, 1988).

Gas Exchange Measurements. Measurements were on the newest fully expanded leaf, closest to the second trellis wire (15th to 20th node on a cane) to minimize shading effects of vine leaves due to the close spacing (0.6 m) within rows. Measurements were made between 1200 and 1500 hrs. Gas exchange was determined with a portable, open system LCA-2 infrared gas analyzer (Analytical Development Company, Hoddesdon, England), combined with an air supply unit (air flow rate 400 cm^3 min^{-1}), and Parkinson broadleaf chamber (6.25 cm^2 window area). The grapevine leaf was non-destructively clamped into the chamber, then the chamber was positioned perpendicular to the incoming solar radiation for approximately 30 seconds (or until equilibration) for determining the following gas exchange variables: A, g_s, E, and WUE. Gas exchange variables were calculated using a BASIC personal computer program (Moon and Flore, 1986).

Abscisic Acid Measurements. Five leaves (removed from nodes 15-20 on each shoot) from each treatment were placed on dry ice immediately after leaves were measured for leaf water potential (ψ_l) (*Liu, et al.*, 1978), on 101 days after planting (DAP) in 1989, and 426, 488, and 502 DAP in 1990, and then transferred to a -20 C freezer. Free (S)-ABA concentrations were determined using a mouse monoclonal antibody to ABA and a radioimmunoassay (EIA) methodology modified from Vernieri *et al.* (1989).

Plant Material. Two-year-old Seyval grapevines (Seyve-Villard 5-276) were grafted on Kober (5BB), Seyval (S/S), or Seyval own rooted (OR) rootstocks were root pruned to 18 cm and planted on May 22, 1989. Planting distances were 0.6 m within rows and 0.9 m between rows. Experimental plots were completely randomized into five single-vine replications per treatment. Vines were trained to a single trunk with two spurs. Two buds per spur were allowed to develop, obtaining a modified pendlebogen trellis system (a low head at the bottom wire).

Irrigation. The first year, vines were drip irrigated at 10 liters per plant per week for 60 days after planting. The second year, vines were drip irrigated at the same level and duration for 60 days, starting on May 22 1990.

Treatments. In 1989, treatments included vines which were defruited at set or maintained at 6 clusters and were irrigated with either 10 liters of water per plant per week as a control, or 2.5 liters of water per plant per week as a drought stress after the first 60 days. In 1990, treatments included vines which were defruited at set or maintained at a maximum of 6 clusters. Irrigation treatments were initiated 60 days after planting for the first year and 60 days after irrigation began May 22, 1990 for the second year and were irrigated with either 10 liters of water per plant per week as a well watered control or 2.5 liters of water per plant per week as a drought stress. Due to excessively cool days early during the 1990 summer, the drought stress vines received 1.8 liters (instead of 2.5 liters) of water per plant per week starting on August 22, 1990.

Soil-Water Content and Matrix Potential. Soil-water moisture data were obtained by a model 503DR hydroprobe, neutron depth moisture gauge (NP). The NP measured sub-

surface soil-moisture through aluminum access tubes, with 5 replications, to a maximum depth of 75 cm in 25 cm cable stop intervals. The NP was calibrated to field conditions according to Chanasyk and McKenzie (1985). The NP recorded a current standard 16 second count format. This count was then changed to soil-water percent moisture by the formula:

$$\theta = 2.42 \cdot 10^{-5} \text{ (counts)} + 0.004$$

$$\theta = 2.42 \cdot 10^{-5} \text{ (counts)} - 0.0036$$

Where "θ" is the soil volumetric moisture content, "counts" is obtained directly from the NP, and 0.004 is the coefficient of a sandy loam soil (depth 0-50 cm of a Kalamazoo soil); 0.0036 is the coefficient of a sandy soil (51-75 cm of a Kalmazoo soil). Soil matrix potential was derived from θ by the formulas:

Soil depth = 25 cm: if $\theta < 0.289$ then $y = 8.84\theta + 2.65$

if $\theta \geq 0.289$ then $y = 62886.19 \cdot 10^{3}\theta\, e^{-70.37\theta}$

Soil depth = 50 cm: if $\theta < 0.236$ then $y = -10.51\theta + 2.58$

if $\theta \geq 0.236$ then $y = 29190.94\theta \cdot e^{-54.07\theta}$

Soil depth = 75 cm: if $\theta < 0.112$ then $y = 24.51\theta + 2.84$

if $\theta \geq 0.112$ then $y = 0.04\theta\, e^{-12.09\theta}$

Where "y" is soil matrix potential (in MPa) $\theta = (0 \leq \theta \leq 1)$.

Leaf Water Potential. Predawn (0400 hrs) ψ_l was measured with a Scholander-type pressure bomb (Plant Moisture Stress Instrument Co.) 101 days after planting (DAP) in 1989, and 426, 488, 502 DAP in 1990. Five fully expanded leaves per treatment were excised with a razor blade and placed so that the leaf petiole extended from the sealed

chamber of the pressure bomb. The pressure was recorded within 30 seconds of leaf removal from the vine when a small amount of xylem exudate appeared on the cut surface of the excised tip of the petiole.

Statistical Analysis. Analysis of variance (ANOVA) was made using the PC version of SAS statistical software (SAS Institute Inc., Cary, N.C.) using a general linear model (GLM) procedure for total gas exchange variables A, g_s, E, and WUE.

RESULTS

1989 Response.

Soil matrix potential (0-75 cm) under the stress (2.5 liters/vine/week) irrigation level was less than the control at 93 DAP August 23, 1989), 32 days after the stress irrigation treatment was implemented, and remained less throughout the experiment (Fig. 1A). The greatest difference in soil matrix potential was in the top 25 cm of soil (Fig. 1B). There were no matrix potential differences at the lower soil depths (Fig. 1C, 1D).

A ψ_l difference between the leaves of the water-stressed vines and that of the controls was detected approximately 101 DAP (October 4, 1989) (Table 1).

There were no differences in gas exchange due to rootstocks, therefore, only effects of water-stress, crop load, and interactions will be reported. Generally, leaves of water stressed vines had a lower A compared to leaves of control vines (Fig. 2A). Leaves of water-stressed vines also had lower g_s (Fig. 2B) and E (Fig. 2C) throughout this experiment. At 95 DAP (August 25, 1989) only, the WUE of the stressed vines was

greater than the control vines (Fig. 2D). There was no difference in A between fruited and defruited vines (data not shown). The g_s (Fig. 3A) and E (Fig. 3B) of fruited vines, however, were greater than defruited vines during mid-season. Defruited vines also had a greater WUE compared to fruited vines during this time (Fig. 3C).

At 95 DAP (August 25, 1989) there was a irrigation x crop load interaction with E (Fig. 4). The water stressed vines responded differently depending on vine crop load. The E of fruited vines under stress irrigation was greater than defruited vines under stress irrigation. The E of the control-irrigated vines responded similarly, regardless if the vines were fruited or not.

There were no crop load effects on leaf ABA content for either year. Therefore, only interactions, water-stress, and rootstock effects are shown. There was a rootstock x crop load interaction at 101 DAP (October 4, 1989) (Table 2). The defruited OR vines had less ABA content than the defruited 5BB and S/S vines. When fruited, both the 5BB and S/S vines had a similar ABA content. The ABA content was greater in water-stressed vines compared to that of the controls at 101 DAP (October 4, 1989) (Table 2).

1990 Response

Soil matrix potential (0-75 cm) under the stress (2.5 liters/vine/week) irrigation was less than the control at 450 DAP (August 15, 1990) and soil remained less throughout the experiment (Fig. 5A). The greatest difference in matrix potential was in the top 25 cm of soil (Fig. 5B). There were differences in matrix potential between water-stressed and control-irrigated plots at the 50 (Fig. 5C) and 75 cm depth (Fig. 5D) later in the

growing season unlike in 1989.

There was a difference between the ψ_l of leaves of the water-stress and the control-irrigated vines at 488 DAP (September 22 1990) and at 502 DAP (October 6 1990) (Table 1.). For both dates, the ψ_l of the stressed vines was more negative than the control vines (Table 1.). There were no rootstock or crop load ψ_l effects.

There were no interactions among treatments for gas exchange variables, nor were there any rootstock or crop load effects during the 1990 growing season. However, leaves of water-stressed vines had lower A (Fig. 6A) compared to control vines beginning 486 DAP (September 20, 1990). The leaves of water-stressed vines had lower g_s (Fig. 6B), E (Fig. 6C), and higher WUE (Fig. 6D) compared to control vines beginning 445 DAP (August 10, 1990). These differences remained relatively the same throughout the experiment.

There was an irrigation x rootstock x crop interaction with leaf ABA content at 488 DAP (October 6, 1990) (Table 2). Most of the rootstocks acted similarly regardless of treatment. The exceptions were the fruited water-stressed S/S vines, which had more ABA levels than the other rootstocks, and the fruited control-irrigated OR vines which had less ABA levels than the other rootstocks. There was an irrigation x rootstock interaction at 488 and 502 DAP (October 6 and 28, 1990). The rootstocks had different ABA levels for water-stress and control treatments. At 488 DAP (October 6, 1990), the S/S vines had the least content of ABA when under water-stress, but all rootstocks had similar content of ABA when under control irrigation. At 502 DAP (October 28, 1990), all 3 rootstocks showed similar leaf ABA content when under water stress. The OR

vines had a greater content of ABA in the leaves than the 5BB and S/S vines when under control irrigation. There was a irrigation x crop load interaction at 502 DAP (October 28, 1990). Under the water-stress irrigation, the ABA level of leaves was greater than ABA level of leaves from control irrigation vines. The leaf ABA level was greater in the water-stressed vines compared to that of the controls at 502 DAP (October 28, 1990) (Table 2). There was a difference in ABA levels of leaves among rootstocks at 488 DAP (October 6, 1990) (Table 2). The ABA level from 5BB leaves was greater than S/S and OR leaves (Table 2), but there was no rootstock difference by 502 DAP. There was no crop load effect.

DISCUSSION

It is clear from these data that water-stress caused a reduction in A, g_s, and E. Uptake of CO_2 (During, 1987) and g_s (Zhang and Davies, 1989) are reduced by water stress. In this study, water-stress caused a reduction in E more than it reduced A, as observed by other researchers (Smart, 1974b; During, 1984; Lakso, 1985). As the water stress continued, the shoot growth and WUE of the stressed vines decreased. Stress symptoms in *V. vinifera* leaves initially are expressed at -0.4 MPa, and tendrils, leaves and berries may abscise (Mathews *et al.*, 1987), but there were no such abscissions in this experiment. Although the water stress was continuous throughout the growing season, the water stress was not severe enough to abscise plant parts.

The data presented in this study did not indicate that a crop load on Seyval grapevines can effect an increase in A. But crop load effects on gas exchange have been reported

in perennial fruit crops (Lakso, 1985), including peaches (Crews *et al.*, 1975), apples (Barden, 1978), cherries (Flore *et al.*, 1985) and grapevines (Chaves, 1984; Williams and Smith, 1985). Kaps and Cahoon (1989), reported that leaves of Seyval grapevines had increased A with increasing cluster numbers at 43 days after full bloom. Increase in A was 60 % higher in vines with three clusters compared to vines with one cluster. Although berry growth has been reported to become an increasingly competitive photoassimilate sink compared to vegetative growth, no differences in A during any year between fruited and defruited vines was observed in this study. Roper *et al.* (1988) reported that in many fruit tree crops (citrus, apple and peach), the effect of fruit on A was dependent on the stage of fruit development. Downton *et al.* (1987) reported that despite heavy crop loads, *V. vinifera* vines showed large diurnal changes in A during rapid berry ripening (phase III). Despite the heavy crop load, the A of the leaves on fruiting vines decreased drastically as the day progressed.

There was no difference between the leaf area of individual leaves of water-stressed or control-irrigated vines in 1990; the 1989 leaf area was not recorded due to an unexpected early frost that damaged the leaves. This is contrary to what other researchers have observed (Hsiao and Jing, 1987; Sharp and Davies, 1979; Westgate and Boyer, 1985; During, 1987; Zhang and Davies, 1989; Bunce, 1990). However, in both years the control vines produced more leaves than water-stressed vines. Although leaf A and not whole plant A was measured, the increase in leaf number probably contributed to the increase of A of the vine during the growing seasons for the control vines. Hsiao and Jing (1987) reported that any increase in leaf area due to expansive growth will result

in increased radiation absorption and more photosynthesis per plant.

In 1989, higher g_s, E, and lower WUE with fruited vines was observed, compared to defruited vines during the first 90 DAP, which agrees with Smart and Coombe (1983). Lakso (1985) reported that crop load generally increased transpiration rates per unit leaf area in perennial fruit crops. This agrees with the 1989 data during the middle of the summer, but does not agree with the 1990 data. No differences for E among fruited and defruited vines was ever observed, but in 1990, the crop load was small for all fruited vines due to the previous years stress, and the crop load of the "heavy load" vines was insufficient to elicit a g_s, or E increase to the vines.

Overall, the ψ_l of the water-stressed vines was roughly twice as negative as that of the controls. As the vine water-stress increased, the ψ_l became more negative. The threshold value of ψ_l for a change in stomatal aperture by *V. vinifera* is about -0.4 MPa (Kriedemann and Smart, 1971; Smart 1974a). The critical ψ_l value for stomatal closure is about -1.3 MPa (Smart, 1974a).

No differences in berry size between the water-stressed or well watered control vines was seen at either year (Chapter III). Berries acquire some resistance to desiccation upon reaching 4 mm in diameter (Hardie and Considine, 1976). The water stress was implemented 60 DAP the first year, well after berry set. The time in which the water stress occurs is important (Hardie and Considine, 1976). The greatest sensitivity appears to be during the lag phase of berry growth (Hardie and Considine, 1976).

Differences in ABA level was related to rootstock selection for both years. At the end of the growing season in 1989, the ABA level of the 5BB and S/S vines was higher

than ABA levels of the OR vines. This would suggest that the vine response to ABA content may not be dependent on its vigor. In 1989, the most vigorous rootstock (based on shoot length) was the OR rootstock. The ABA level in the leaves of OR vines was lower than leaves grafted to 5BB or S/S rootstocks. In 1990, the 5BB and OR rootstocks were more vigorous than the S/S rootstock and the ABA level of the leaves from 5BB rootstocks was greater than the S/S vines. In previous work (Fregoni *et al.*, 1978) drought resistant rootstocks 420A, 99R, and 1103P had higher levels of ABA than in drought sensitive vines such as the 5BB. The 1989 and 1990 results differ from their findings. The 5BB vines, being drought sensitive, should have had less ABA content in the leaves compared to the more vigorous OR vines of 1989 and 1990. Accumulation of ABA in grapevine leaves, associated with soil drying improves WUE but inhibits A directly (Downton *et al.*, 1987).

In both years, matrix potential was more negative at the shallowest depths. In both years, as the soil matrix potential became more negative for water-stressed treatment, the A, g_s, and E of the vines also decreased. In 1989 the A, g_s, and E, of the water stressed vines was less than the control irrigated vines at about 2 weeks after the water stress was implemented. In 1990 it was 2 months after the water stress treatment was implemented that a decrease in A, gs, and E was observed. The vines were older, well established, and had a better developed root system, which contributed to the vines ability to resist the soil-water reduction by accessing water in the lower depths as indicated by differences in soil matrix potential in 1990, unlike 1989.

CONCLUSIONS

1. A, g_s, and E, of leaves on water-stressed vines were reduced, and WUE was increased compared to control-irrigated grapevines.
2. ABA content of leaves was increased by water-stress. ABA probably was responsible for reductions in A, g_s, and E due to stomatal closure, as the critical value for ψ_l was not reached.
3. Water-stress affected grapevine leaf g_s greater than A.
4. Established vines were more tolerant to water stress compared to newly established vines due to more extensive root system (Chapter III).

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CAPTIONS FOR FIGURES

Figure 1. The 1989 matrix potential (in MPA) of a Kalamazoo type soil (fine-loamy, mixed mesic Typic Hapludolfs) under a rain-exclusion shelter in Michigan. The letters "WS" represent the date of implementing the water stress treatment (July 22, 1989). (A) Overall 25-75 cm depth of matrix potential of stress (2.5 liters of water per vine per week) and control (10 liters of water per vine per week) irrigated 2-year-old Seyval grapevines, (B) Matrix potential at 25 cm depth, (C) Matrix potential at 50 cm depth, (D) Matrix potential at 75 cm depth. Each value represents the mean of five replications. Vertical lines represent SE.

Figure 2. The 1989 gas exchange of water-stressed and control-irrigated Seyval grapevines. The letters "ws", "v", "h", and "ld" refer to the dates of (implementing) the water stress treatment (July 22, 1989), veraison (August 18, 1989), fruit harvest (September 28, 1989), and leaf drop (October 9, 1989) respectively. (A) Net Co_2 Assimilation (A), (B) stomatal conductance (g_s). Each value represents the mean of thirty vines, (C) Transpiration (E), (D) water use efficiency (WUE). Each value represents the mean of thirty vines. Vertical lines represent SE.

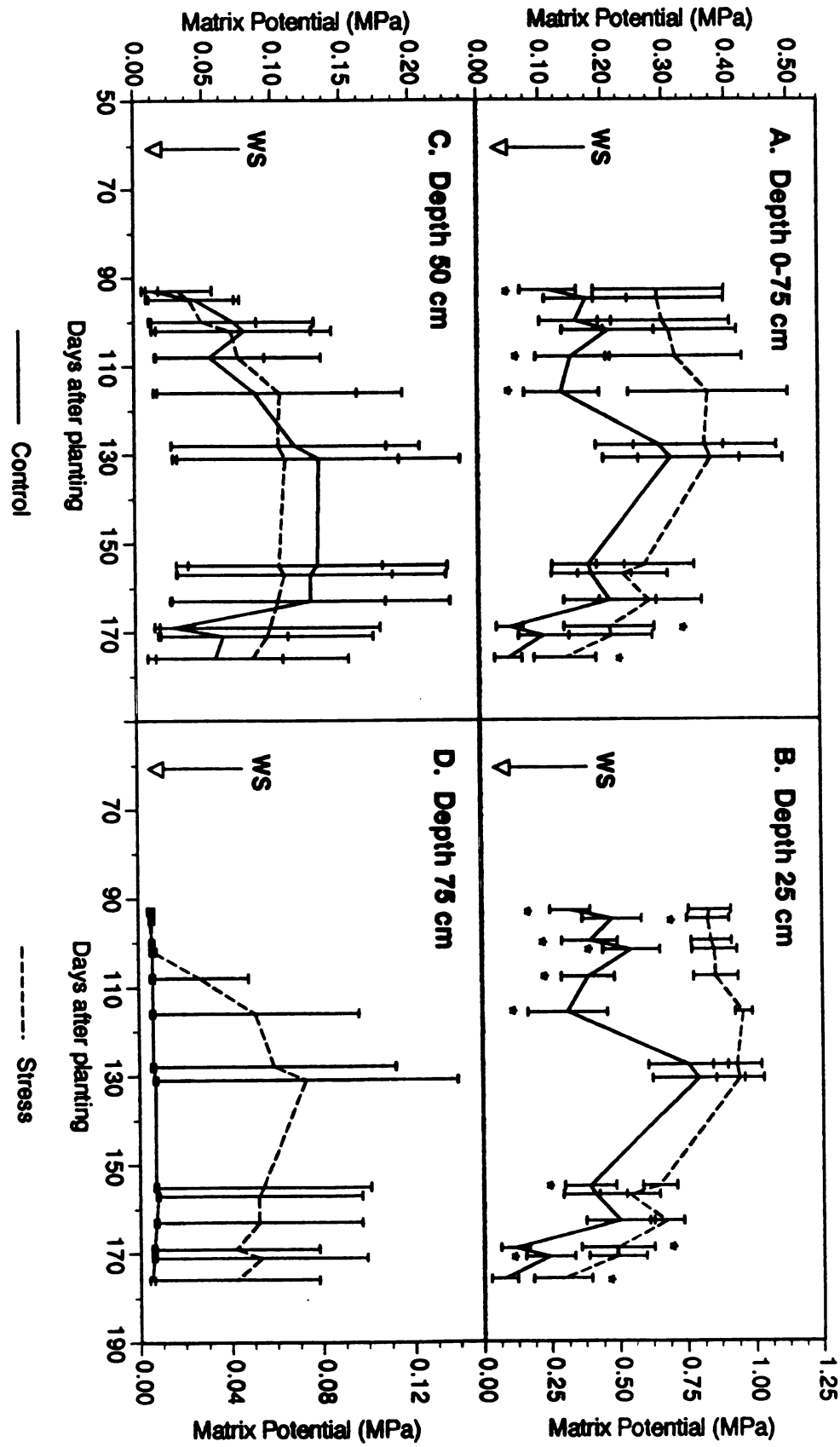
Figure 3. The 1989 gas exchange of defruited and fruited Seyval grapevines. (A) stomatal conductance (g_s), (B) Transpiration (E), (C) water use efficiency (WUE). The letters "ws", "v", "h", and "ld" refer to the dates of (implementing) the water stress treatment (July 22, 1989), veraison (August 18, 1989), fruit harvest (September 28, 1989), and leaf drop (October 9, 1989) respectively. Each value represents the mean of thirty vines. Vertical lines represent SE.

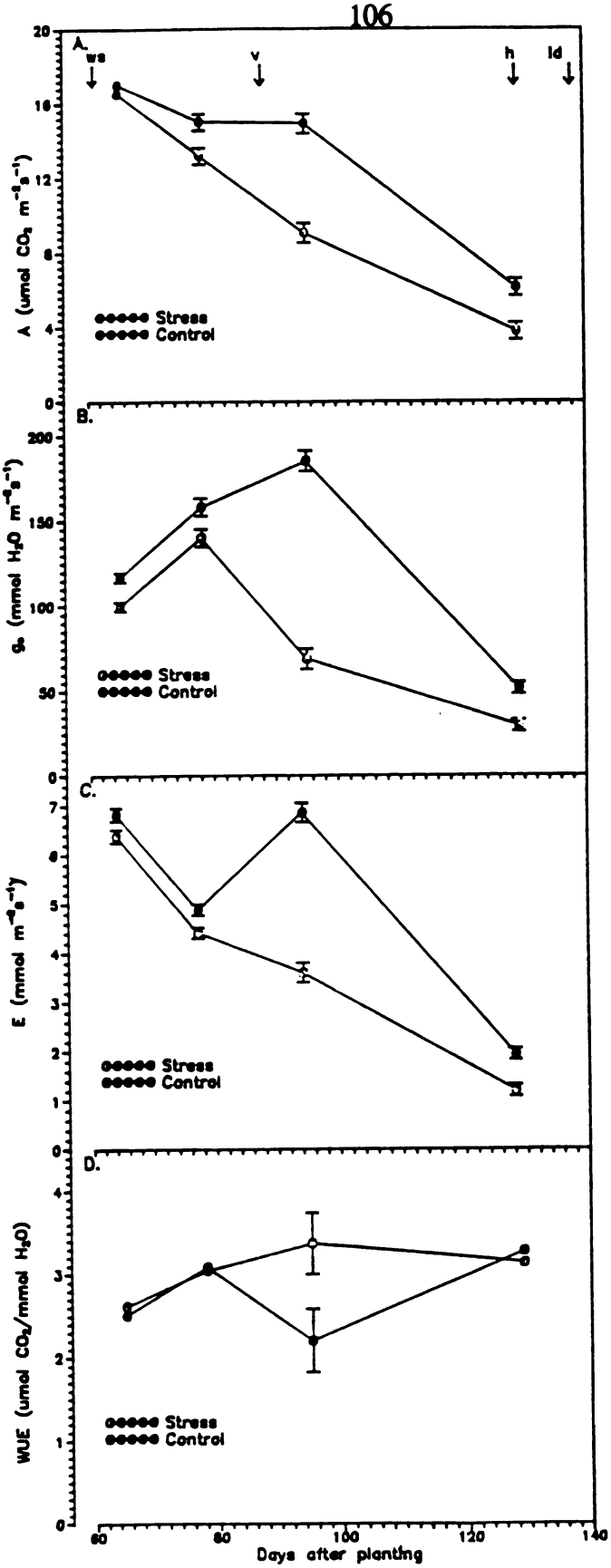
Figure 4. The 1989 gas exchange transpiration (E), of the interaction between irrigation and crop load in Seyval grapevines. The letters "ws", "v", "h", and "ld" refer to the dates of (implementing) the water stress treatment (July 22, 1989), veraison (August 18, 1989), fruit harvest (September 28, 1989), and leaf drop (October 9, 1989) respectively. Each value represents the mean of fifteen vines. Vertical lines represent SE.

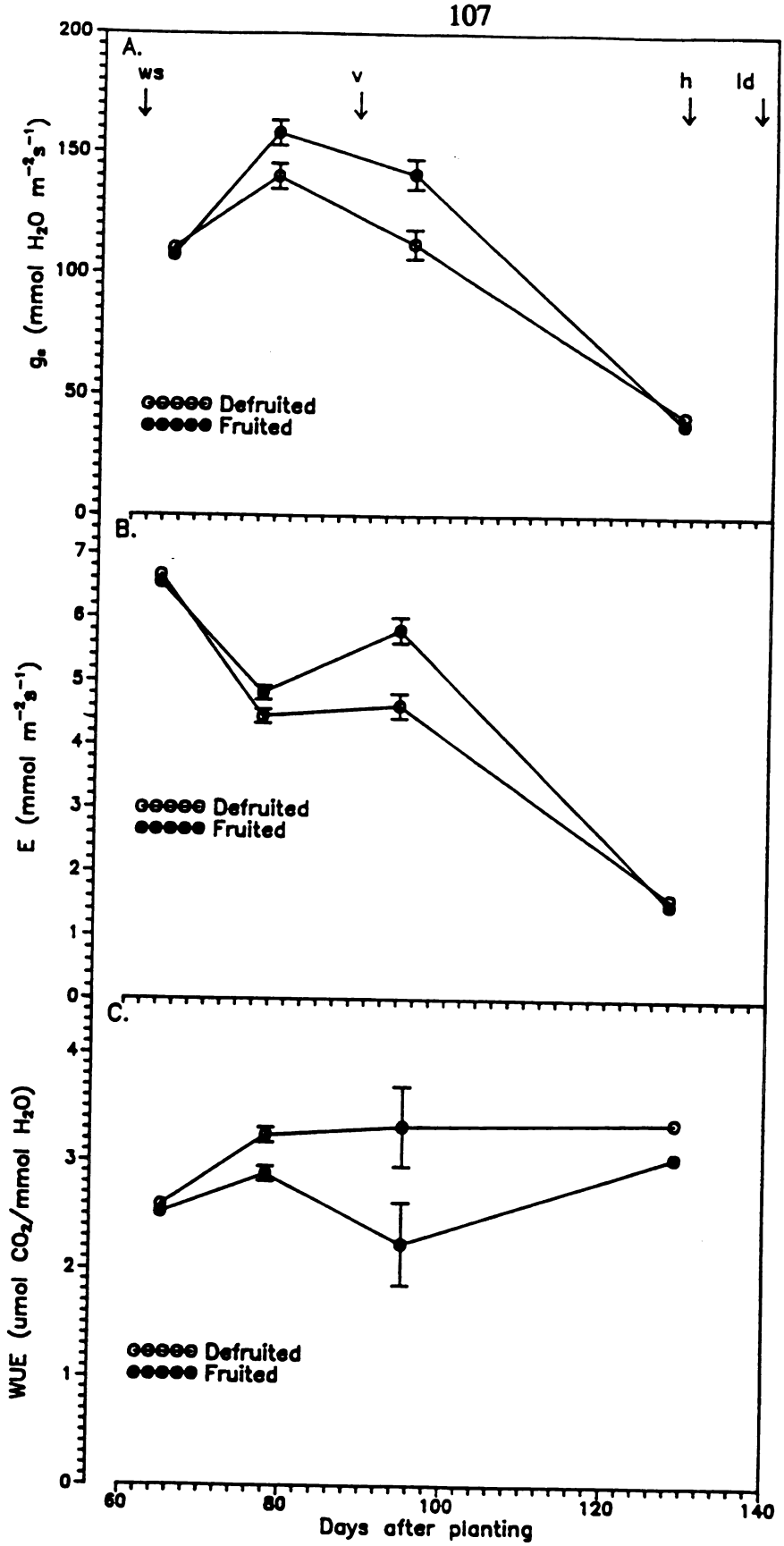
Figure 5. The 1990 matrix potential (in MPa) of a Kalamazoo type soil (fine-loamy, mixed mesic Typic Hapludolfs) under a rain-exclusion shelter in Michigan. The letters "WS" represent the date of implementing the water stress treatment (July 22, 1989). (A) Overall 25-75 cm depth of matrix potential of stress (2.5 liters of water per vine per week, this was reduced to 1.8 liters of water per vine on 8/22/90) and control (10 liters of water per vine per week) irrigated 2-year-old Seyval grapevines, (B) Matrix potential at 25 cm depth, (C) Matrix potential at 50 cm depth, (D) Matrix potential at 75 cm

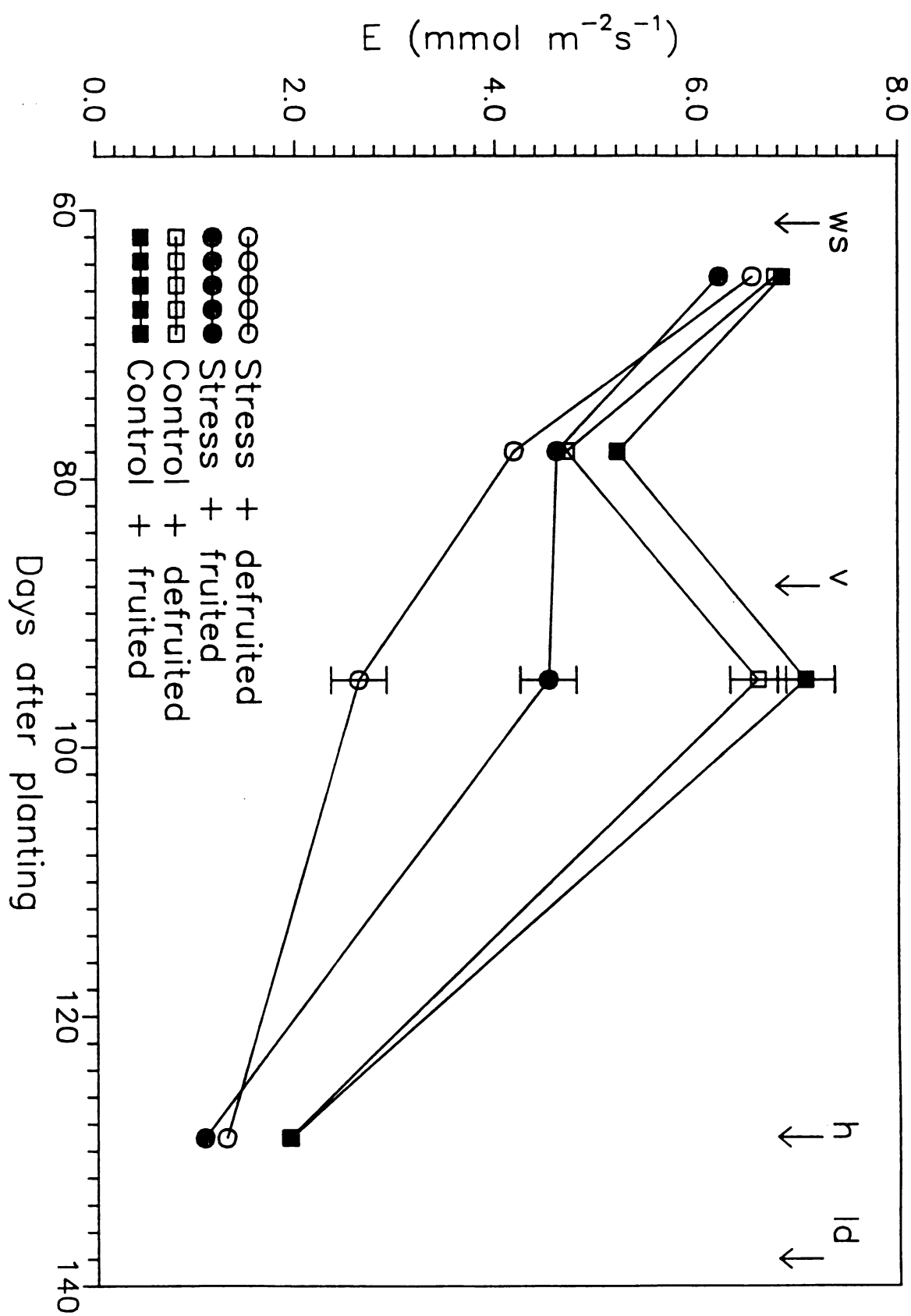
depth. Each value represents the mean of five replications. Vertical lines represent SE.

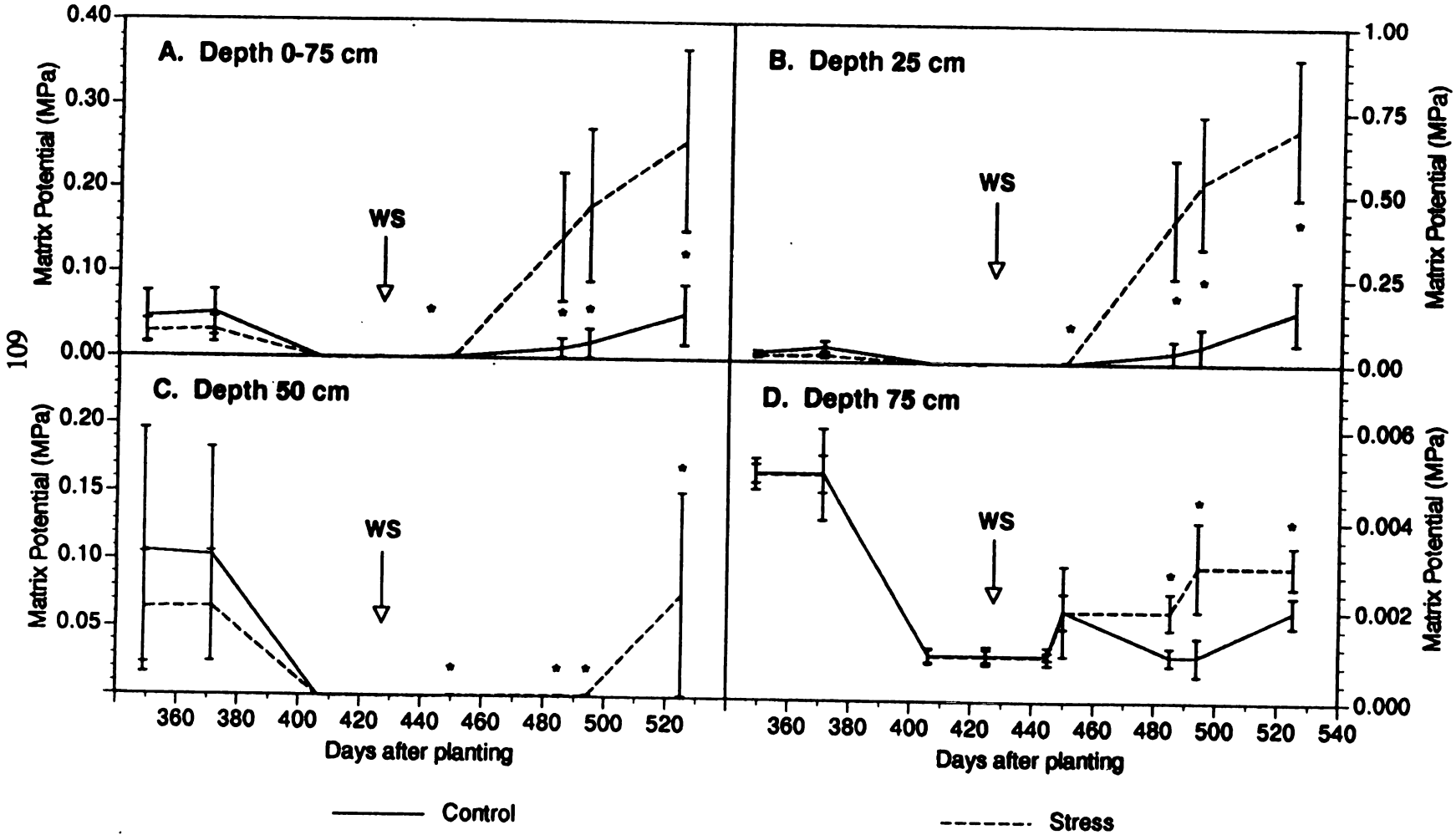
Figure 6. The 1990 gas exchange of water-stressed and control-irrigated Seyval grapevines. The letters "bb", "b", "ws", "v", and "h" refer to the dates of bud burst (May 6, 1990), bloom (June 6, 1990), (implementing) the water stress treatment (July 22, 1990), veraison (August 22, 1990), and fruit harvest (September 21, 1990), respectively. (A) net CO_2 Assimilation (A), (B) stomatal conductance (g_s), (C) transpiration (E), (D) water use efficiency (WUE). Each value represents the mean of thirty vines. Vertical lines represent SE.


A. Depth 0-75 cm
B. Depth 25 cm
C. Depth 50 cm
D. Depth 75 cm
WS
Matrix Potential (MPa)
Days after planting
Control
Stress


A.
ws
v
h
ld
A (umol CO2 m-2s-1)
Stress
Control
B.
gs (mmol H2O m-2s-1)
Stress
Control
C.
E (mmol m-2s-1)
Stress
Control
D.
WUE (umol CO2/mmol H2O)
Stress
Control
Days after planting


A.
ws
v
h
ld
g_s (mmol H_2O $m^{-2}s^{-1}$)
200
150
100
50
0
Defruited
Fruited
B.
E (mmol $m^{-2}s^{-1}$)
7
6
5
4
3
2
1
0
Defruited
Fruited
C.
WUE (umol CO_2/mmol H_2O)
4
3
2
1
0
Defruited
Fruited
60
80
100
120
140
Days after planting


E (mmol m^{-2}s^{-1})
0.0
2.0
4.0
6.0
8.0
60
80
100
120
140
Days after planting
Stress + defruited
Stress + fruited
Control + defruited
Control + fruited
ws
v
h
pl


A. Depth 0-75 cm
B. Depth 25 cm
C. Depth 50 cm
D. Depth 75 cm
WS
Matrix Potential (MPa)
Days after planting
Control
Stress

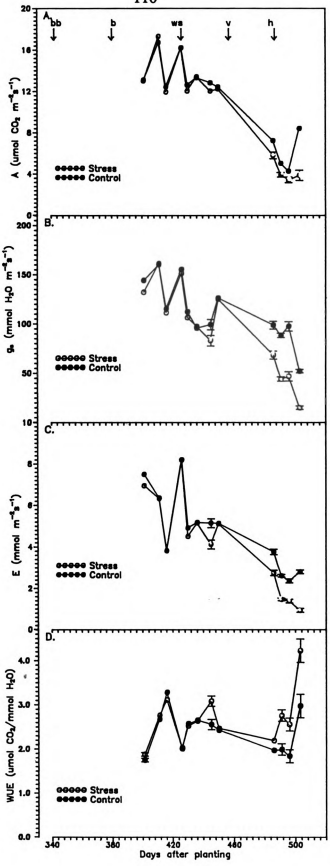

A.
bb
b
ws
v
h
A (umol CO2 m-2s-1)
Stress
Control
B.
gs (mmol H2O m-2s-1)
Stress
Control
C.
E (mmol m-2s-1)
Stress
Control
D.
WUE (umol CO2/mmol H2O)
Stress
Control
340
380
420
460
500
Days after planting

Table 1. Effects of 1989 and 1990 irrigation, rootstock and crop load on Leaf Water Potential ψ_l (MPa) of Seyval grapevines by dates and days after planting.

	10/4/89 101 DAP	10/6/90 488 DAP	10/28/90 502 DAP
Irrigation			
Stress[x]	4.21	4.5	6.4
Control[y]	1.71	2.0	2.8
	***[z]	***	***
Rootstock			
5BB	3.06	3.2	4.7
S/S	2.81	3.3	4.7
OR	3.01	3.1	4.5
	N.S.	N.S.	N.S.

[z] **, ***, NS, Significant at P = 0.01, 0.001, or nonsignificant, respectively.
[y]1989 and 1990 irrigated 10 liters of water/plant/week.
[x]1989 irrigated 2.5 liters of water/plant/week. 1990 irrigated 2.5 liters of water/plant/week; on 8/22/90 irrigation was deceased to 1.8 liters of water/plant/week.

Table 2. Effects of 1989 and 1990 irrigation, rootstock and crop load on leaf abscisic level (ng/g dry leaf weight) of Seyval grapevines by days after planting (DAP).

	101 DAP	488 DAP	502 DAP
Irrigation			
Stress[y]	81	101	142
Control[z]	64	101	92
LSD 0.05	11	N.S.	9
Rootstock			
5BB	75	111	112
S/S	80	95	115
OR	62	98	124
LSD 0.05	13	7	N.S.
Irrigation x Rootstock			
Stress			
5BB	81	114	145
S/S	88	89	142
OR	72	100	140
Control			
5BB	70	107	79
S/S	71	100	88
OR	52	96	109
LSD 0.05	N.S.	10	16
Irrigation x Crop Load			
Stress			
0 cluster	76	102	137
6 cluster	85	101	147
Control			
0 cluster	64	101	101
6 cluster	64	101	83
LSD 0.05	N.S.	N.S.	20
Rootstock x Crop Load			
Seyval/5BB			
0 cluster	73	107	116
6 cluster	77	115	108
Seyval/Seyval			
0 cluster	87	97	116
6 cluster	72	92	114
Seyval Own Root			
0 cluster	50	100	126
6 cluster	75	96	123
LSD 0.05	19	N.S.	N.S.
Irrigation x Rootstock x Crop Load			
Stress, Seyval/5BB			
0 cluster	84	110	145
6 cluster	78	119	146
Stress, Seyval/Seyval			
0 cluster	94	98	133
6 cluster	82	80	151
Stress, Seyval/Own			
0 cluster	49	98	135
6 cluster	96	103	145
Control, Seyval/5BB			
0 cluster	62	104	88
6 cluster	76	111	70
Control, Seyval/Seyval			
0 cluster	80	96	99
6 cluster	61	104	78
Control, Seyval/Own			
0 cluster	50	103	117
6 cluster	54	89	101
LSD 0.05	N.S.	14	N.S.

[y]1989 irrigated 2.5 liters of water/plant/week. 1990 irrigated 2.5 liters of water/plant/week, reduced to 1.8 liters water/plant/week 457 DAP.
[z]1989 and 1990 irrigated 10 liters of water/plant/week.