Effects of Light, Temperature, Defoliation, and Fruiting on Carbon Assimilation and Partitioning in Potted Cranberry

Justine E. Vanden Heuvel
University of Massachusetts Amherst, Cranberry Experiment Station, 1 State Bog Road, P.O. Box 569, East Wareham, MA 02538

Joan R. Davenport
Washington State University, Irrigated Agriculture Research and Extension Center, 24106 North Bunn Road, Prosser, WA 99350

Abstract. Carbohydrate supply has been hypothesized to limit fruit set in cranberry (Vaccinium macrocarpon Ait.), however the limitations to carbon gain throughout the season are currently unknown. These experiments investigated the effects of light, temperature, fruit presence, and defoliation on carbon production and partitioning in potted cranberry. Fruiting and vegetative uprights (short vertical stems which bear fruit biennially) reached similar asymptotes with respect to light response, but fruiting uprights reached saturation at a lower light intensity than vegetative uprights. Runners (diageotropic vegetative stems) had a lower asymptote, higher light compensation point, and greater rate of dark respiration than uprights. Temperature had little effect on net carbon exchange rate of uprights or runners. Before new growth, defoliation did not affect the concentration of total nonstructural carbohydrates in the vegetative uprights, or the partitioning of soluble carbohydrates to starch, even though uprights with lower leaf areas had higher net CO2 assimilation. At fruit set and again at fruit maturity, defoliation reduced total nonstructural carbohydrates in the vegetative uprights, or the partitioning of soluble carbohydrates to starch, while net CO2 assimilation was not affected. Carbohydrate production and partitioning within an upright was unaffected by the presence of a single fruit throughout the experiment.

Materials and Methods

Experiment 1: Light and temperature response

Plant material. Actively growing ‘Stevens’ cranberry uprights were collected from the University of Massachusetts Amherst Cranberry Experiment Station research bog (State Bog), E. Wareham, Mass. (Lat.: 41°45’ N, Long.: 70°40’ W) in May 2003. Four nonrooted cuttings, 10 cm in length, were planted in a 10-cm pot containing 50:50 (v:v) of sand (collected from State Bog) and ‘Berger’ peatmoss (R.F. Morse, Wareham, Mass.). Pots were irrigated daily using overhead mist. Osmocote slow release fertilizer (14N–6P–11K) was applied to the surface of the soil mix 4 weeks following planting. Flowers were removed to prevent fruit production. Vines were stored in the dark over the winter at 3 ± 1 °C for a period of 16 weeks to induce dormancy. In March 2004, they were placed in a greenhouse under ambient temperature and light conditions.

Treatments. In July 2004, 17 vegetative uprights, 17 fruiting uprights from randomly selected plants were subjected to varying temperature levels (20, 23, 26, 29, 32 °C) in the monitoring chamber, or to varying levels of PAR (about 0, 500, 700, 1100, 1500, 2000, 2500 μmol·m−2·s−1) using a high pressure sodium (HPS) greenhouse lamp. Fruiting uprights had either one or two fruit per upright. Net carbon exchange rate (NCER) of uprights was measured using a CIRAS-2 portable infrared gas analyzer connected to an automated PLC5(C) conifer cuvette (PP Systems, Amesbury, Mass.). The chamber temperature was maintained at 25 °C during light response work. Air flow was 400 mL·min−1 with CO2 maintained at 360 ± 10 ppm. The chamber was clamped around the top 10 cm of the upright for 5 min, then measurements of NCER were taken every 15 s until a steady rate (±0.2 μmol·m−2·s−1) was reached (about 1 min).

Data analysis. Equations for temperature response were generated using a non linear regression modeling program (PC SAS Proc NLIN, SAS Institute, Cary, N.C.), in the form of

\[ Y = a – b e^{cx} \]  

where \(a\) = asymptote, \(b\) = intercept, \(c\) = rate of approach to asymptote, and \(x\) = the x-axis value. Light response data were fitted to the model

\[ Y = a – b e^{cx} \]  

following Proctor et al. (1976), where \(a\) = asymptote, \(b\) = intercept, \(c\) = rate of approach to asymptote, and \(x\) = the x-axis value. The \(r^2\) for the light response curves were approximated by hand by dividing model sum of squares by the corrected total sum of squares (Steel et al., 1997). Respiration rate was calculated using Eq. 2 by setting \(X = 0\), and light compensation point was calculated by setting \(Y = 0 \) and solving for \(X\) based on Eq. 2, so that

\[ X = -1/c \times \ln(a - y/b) \]

where \(a\) = asymptote, \(b\) = intercept, \(c\) = rate of approach to asymptote, and \(x\) = the x-axis value. Model assumptions were tested through residual analysis and were determined to have been met.
Treatments. Treatments were 0%, 25%, 50%, or 75% defoliation of both current and 1-year-old leaves, and 0 or 1 fruit per upright. Fruiting treatments were not imposed; uprights were chosen for the study based on whether they were vegetative or had a single fruit. Each set of treatments was applied at one of three phenological stages: 1) before new vegetative growth on the upright, 2) fruit set, and 3) fruit maturity. Before new growth, there were no fruit or flowers on the upright, resulting in the application of only the four defoliation treatments. Each treatment was applied to four replicate pots, with four uprights per pot. Pots were arranged in a randomized complete block design. Uprights were grown under ambient light conditions (maximum 1000 µmol·m⁻²·s⁻¹ PPF on sunny days). Leaf area removed per measurement upright was quantified using a leaf area meter (LI-3100; LI-COR, Lincoln, Neb.).

Data collection. Photosynthesis of individual uprights was quantified on a leaf area basis before defoliation, and 24 h (day 1), 72 h (day 3), and 144 h (day 7) following defoliation. Data collection with regards to carbon assimilation was similar to the method described in Expt. 1. Measurements were made in the morning to avoid excessive greenhouse temperatures, and were completed between 0730 and 1030 h. About 700 µmol·m⁻²·s⁻¹ PPF was supplied to the uprights during measurement using a HPS light source. Although photosynthesis in uprights is likely affected by inter-leaf shading, an irradiance of 700 µmol·m⁻²·s⁻¹ PPF can result in 90% of maximum NCER in field-grown Stevens vines (Hagidimitriou, 1993). Vines were measured in a randomized complete block × replication to remove variation due to increasing temperature with time in the greenhouse. For nonfruited uprights, the conifer cuvette (chamber) was clamped onto the top 10 cm of the upright. On fruited uprights the chamber was clamped immediately above the fruit (about 10 cm). Tissue acropetal to developing flowers and fruit are the primary source of photosynthates for reproductive development (Roper and Klueh, 1996). Temperature and vapor pressure deficit (VPD) in the chamber were not controlled, as we were concerned that varying these factors on only a portion of the upright (inside the conifer chamber) might lead to water potential differences that could affect assimilation and/or partitioning. Air flow was 400 mL·min⁻¹ with CO₂ maintained at 360 ± 10 ppm. The chamber was clamped around the upright for 5 min, then measurements of NCER were taken every 15 s until a steady rate (±0.2 µmol·m⁻²·s⁻¹) was reached. At each of the three phenological stages, NCER at 1, 3, and 7 d following defoliation were very similar, and therefore only predefoliation and 3, and 7 d following defoliation were very similar, and therefore only predefoliation and 24 h (day 1), 72 h (day 3), and 144 h (day 7) following defoliation were very similar, and therefore only predefoliation and 7 d data are presented.

After each sampling time, fruit, shoots, and roots were separated and dried at 80 °C for 5 d, weighed, and ground to 40 mesh using a Wiley mill. In the fruited treatments, the number of uprights per pot that actually set fruit ranged from 1 to 4. When there were fewer than four fruited uprights in any replication, defoliation level was still applied to all uprights; however carbohydrate concentrations were quantified only on tissue of fruit-bearing uprights. Thus, in a number of instances, there was insufficient root (i.e., below ground) tissue for HPLC analysis.

Concentrations of starch, sucrose, fructose, and glucose in uprights and roots were determined using high performance liquid chromatography (Botelho and Vanden Heuvel, 2005). Briefly, 100 µg subsamples were triple-extracted in 5 mL of 80% EtOH for 1 h at 54 °C. The extract was filtered, dried at 54 °C, and the solids were saved for starch analysis. The dried extract was reconstituted in 5 mL HPLC-grade H₂O (Fisher Scientific, Pittsburgh, Pa.), filtered, then passed through a conditioned Sep-Pak Plus C₁₈ cartridge (Waters Corp., Milford, Mass.). The dried solid sample remaining after extraction was resuspended in 5 mL H₂O and autoclaved at 250 °C for 30 min, allowed to cool, and 100 µL amylglucosidase (Sigma Chemical, St. Louis, Mo.) in buffer solution (pH = 4.63) was added. The samples were incubated at 54 °C in a water bath for 2 h, filtered, and passed through a conditioned Sep-Pak Plus C₁₈ cartridge. Starch concentration was measured in glucose equivalents. Samples were analyzed using a ‘Breeze’ HPLC system (Waters Corp.). The mobile phase was 80 °C HPLC-grade water. Samples were maintained at 8±1 °C in the autosampler, and run through a Shodex SC1011 (Waters Corp.) ion-exchange column, and a refractive index detector at 40 ± 1 °C. Total tissue carbon (C) and nitrogen (N) were analyzed by dry combustion according to the methods of Nelson and Sommers (1996) and Bremner (1996) on a LECO CNS analyzer (St. Joseph, Mich.) and expressed on a percentage of dry weight.

Data analysis. Analyses of variance and regression analyses were conducted using PC SAS PROC GLM (SAS Institute, Cary, N.C.). Data for carbohydrate concentration were related to average leaf area per upright in each pot, while NCER was related to the leaf area of the measured upright.

Results and Discussion

Light response curves. Light response curves generated for potted uprights and runners differed, particularly at lower light intensities (Fig. 1). While fruited and vegetative uprights eventually reached similar asymptotes, fruiting uprights approached the asymptote more quickly than did vegetative uprights, indicating fruiting uprights have a higher quantum yield and can likely capitalize on the existing light microclimate in the field. In a crowded canopy, these differences may be significant with respect to carbon assimilation of the whole vine. The asymptote of the light response curve for runners was much lower than for the uprights, indicating that runners are unable to make as significant a contribution as uprights to leaf area basis to total vine carbon assimilation. Field-grown ‘Stevens’ uprights have been demonstrated to be photosynthesizing at 90% maximum NCER at an irradiance of 700 µmol·m⁻²·s⁻¹ PPF (Hagidimitriou, 1993), although this work did not differentiate between fruiting and vegetative uprights. In our study, fruiting uprights were operating at 97% of maximum NCER at 700 µmol·m⁻²·s⁻¹ PPF, while vegetative uprights and runners operated at 82% and 84%, respectively, of maximum NCER. It is noteworthy that inter-leaf shading was likely minimized on the runners during measurements, as runner leaves tend to be very well-spaced along the stem compared to upright leaves. Due to inter-leaf shading,
values of NCER of uprights are likely more representative of whole-canopy measurements than single leaf measurements.

Runner leaves had a greater rate of dark respiration (Rd) (~1.18 µmol CO₂/m²/s) than did fruiting and vegetative leaves (Rd = –0.49 and –0.45 µmol CO₂/m²/s, respectively). This greater rate of Rd demonstrated by runner leaves is interesting, considering the lower NCER. It is unknown if there are differences in anatomy, nitrogen content or carbohydrate production between runner and upright leaves.

Light compensation point also differed between upright and runner tissue. The light compensation points for fruiting uprights, vegetative uprights, and runners were 15.3, 28.6, and 103.2 µmol·m⁻²·s⁻¹, respectively. The differences between light compensation point for uprights and runners could be due to the effect of inter-leaf shading on the shape of the light response curve as the rate of approach to the asymptote was greater for uprights than for runners, or due to the higher rate of Rd in runner leaves.

Temperature response curves. A temperature response curve for cranberry uprights has not been previously reported, although Kumudini (2004) concluded that calculated quantum yield for individual ‘Stevens’ leaves did not differ between 15 to 35 °C. We also found little response of NCER to temperature between 20 to 32 °C (data not shown), although these data contained a great deal of variability among replicate plants. Temperature response of cranberry vines requires further investigation to determine optimal field temperatures, as well as optimal temperatures for future carbon exchange studies.

Effect of defoliation before new growth. Uprights with lower leaf area (LA) had higher NCER (Fig. 2A) before defoliation. As this was a measurement of previous year growth on the upright, and older leaves are reasonably well-spaced, it is unlikely that the higher NCER on uprights with lower LA is due to reduced shading of leaves. There was not a significant relationship between LA and stomatal conductance (gₛ) (Fig. 2B) or internal CO₂ concentration (Cᵢ) before defoliation (Fig. 2C), indicating that NCER was not limited by those variables. Upright N concentration showed a slight but nonsignificant increase with decreased leaf area (data not shown) and may have partially contributed to the increased NCER demonstrated by uprights. Following defoliation, the relationship between NCER and LA was maintained up to 7 d (Fig. 2D) and was coupled with gₛ (Fig. 2E) and Cᵢ (Fig. 2F). Differences in mean NCER, gₛ, and Cᵢ during the experiment were likely due to differences in air and leaf temperature, as leaf temperature and VPD differed between measurement dates (26.3 °C and 1.7 kPa at day 0, and 23.0 °C and 1.1 kPa at day 7). The NCER and gₛ of the control treatment leaves were similar over the 7-d period, indicating that there was not a significant time effect.

Soluble carbohydrates, starch, and TNSC were not significantly affected by defoliation before new growth (data not shown; r² < 0.05), indicating a possible sink-limitation to carbohydrate production at this stage. The TNSC concentration ranged from 2 to 6 mg/100 mg, lower than the 7 to 8 mg/100 mg TNSC reported for vegetative field-grown uprights early in the season (Hagidimitriou and Roper, 1994). Carbohydrate concentrations reported here are likely lower due to the use of young greenhouse-grown vines.

Increased NCER did not result in increased soluble carbohydrate concentration, starch concentration, or TNSC concentration in the roots (data not shown, r² < 0.10). Roots accounted for very little of the total plant TNSC, as root TNSC ranged from 0.6 to 0.8 mg/100 mg. This finding is consistent with previous work which indicated that below-ground tissue accounted for only 10% of total vine TNSC (Hagidimitriou and Roper, 1994; Botelho and Vanden Heuvel, 2005). Roots did, however, have a higher C:N ratio than upright tissue (Table 1).

These results indicate a possible sink-limitation to carbon production at the start of the growing season. Leaves may not have been photosynthesizing at their maximum capacity, as evidenced by the stimulation of gₛ, and Cᵢ by defoliation and the inverse relationship between NCER and LA before defoliation. Net CO₂ assimilation was not coupled to gₛ, and Cᵢ before defoliation, suggesting that other factors were limiting photosynthesis early in the season. The inability of increased NCER to improve TNSC in the uprights or roots suggests a limitation in carbon production and/or storage.

Effect of defoliation and fruit presence at mid-season (i.e., fruit set). Before defoliation, there was no significant effect of LA on NCER, gₛ, or Cᵢ (data not shown; r² < 0.05). Seven days after defoliation, there was no effect of LA on NCER or gₛ (data not shown; r² < 0.01), and only a weak relationship between Cᵢ and LA (r² = 0.41). Leaf temperature and VPD (26.6 °C vs. 32.8 °C, 1.5 kPa vs. 2.4 KPa) were lower on day 0 than day 7, with leaves on day 7 probably temperature stressed. However, at 72-h postdefoliation (leaf temperature = 27.0 °C, VPD = 1.6 kPa), the relationship between LA and NCER (as well as of LA-gₛ and LA-Cᵢ) was the same as on day 7 (data not shown).

These results suggest that the leaves were...
operating at their maximum capacity, with a possible source-limitation to carbohydrate production at fruit set, in agreement with previous works (Birrenkott and Stang, 1990; Roper et al., 1992).

Fruiting had no effect on NCER in a previous experiment in cranberry (T.R. Roper, unpublished data) and has variable effects in other crops. The mean NCER in vegetative and fruiting uprights was similar before defoliation (3.6 and 4.3 µmol·m⁻²·s⁻¹ for vegetative and fruiting uprights, respectively). A similar response was also evident following defoliation (4.6 and 5.2 µmol·m⁻²·s⁻¹). The slightly higher NCER of single-fruited uprights suggests that with two fruit on an upright (which is common on vigorous, well-managed beds or fields), leaves on fruiting uprights may have the photosynthetic capacity to improve NCER to partially meet increased sink demand at fruit set. As well, measurements taken early in the morning, such as in this experiment, may not accurately reflect sink strength throughout the day (Downton et al., 1987; Gucci, 1988), although defoliated grape vines have demonstrated differences in NCER between fruiting and nonfruiting shoots, regardless of time of measurement (cited by Flore and Lakso, 1989).

Net CO₂ assimilation in field-grown cranberry peaks 2 to 3 h after sunrise (Hagidimitriou and Roper, 1995).

Concentrations of soluble carbohydrates, starch, and TNSC were all slightly reduced by defoliation at fruit set (data not shown; \( r^2 = 0.25, 0.24, \) and 0.30, respectively). Combined with the lack of stimulation in NCER or gs by defoliation at this time, these results suggest a significant source limitation in carbohydrate production once fruiting begins. The TNSC at this time was lower than TNSC concentration of old growth before flowering, in agreement with earlier studies (Birrenkott et al., 1991; Hagidimitriou and Roper, 1994).

The mean concentration of TNSC in fruiting and vegetative uprights was 2.9 and 2.6 mg/100 mg, respectively (\( P = 0.055 \)), and these differences between upright types may be due to small differences in starch concentration (1.1 and 0.9 mg/100 mg, respectively, \( P = 0.034 \)). It is possible that roots and expanding leaves are strong sinks for photoassimilates in vegetative uprights, allowing fruiting uprights to remove assimilates from photosynthetic sites to the same degree as in fruiting uprights.

The concentration of TNSC in roots was 1.3 to 1.5 mg/100 mg at this growth stage in the limited samples available. There was insufficient root material to establish if there was a relationship between root carbohydrates and LA.

**Effect of defoliation and fruit presence at fruit maturity.** LA did not significantly affect NCER at fruit maturity (data not shown), although \( C_i \) was increased by defoliation (\( r^2 = 0.72 \)). The NCER, \( g_s \), and \( C_i \) of the control treatment leaves were similar between measurement dates, indicating the lack of a significant time effect. Leaf temperature (27.6 vs. 24.5 °C) and VPD (1.9 vs. 1.5 kPa) were higher on day 7 than on day 0. These results were similar to those found at fruit set. The uncoupling of NCER from \( g_s \) and \( C_i \) during this growth stage indicates that the stomata are...
not limiting NCER. The response of cranberry stomata to environmental conditions is weak (Croft et al., 1993).

Concentration of soluble carbohydrates reached an asymptote (Fig. 3A), while starch and TNSC were very weakly (and linearly) related to LA (Fig. 3B and C), suggesting that as LA on an upright increases, more C may be partitioned to starch. Growing vines under enhanced CO2 also increases C partitioning to starch (T.R. Roper, unpublished data). It is not known whether increased starch could be used as a source for fruit growth. Fruiting uprights had lower NCER than vegetative uprights before defoliation (2.9 and 3.6 µmol·m⁻²·s⁻¹ for fruiting and vegetative uprights, respectively, \(P = 0.028\)). This difference may be attributed to slightly lower stomatal conductance in fruiting uprights (59.2 and 70.5 mmol·m⁻²·s⁻¹ for fruiting and vegetative uprights, respectively, \(P = 0.054\)). To our knowledge, a negative fruiting effect on NCER has not been demonstrated previously in a fruit crop. These fruiting differences were visible throughout the week following defoliation, however they were only significant at 72 h (2.2 and 3.1 mmol·m⁻²·s⁻¹ for fruiting and vegetative uprights, respectively, \(P = 0.011\)). The lower NCER of fruiting uprights cannot be attributed to reduced N concentration (Table 1). It is possible that there may have been an increase in vegetative sink activity that would account for these differences in NCER. It is unlikely that the decreased NCER of fruiting (vs. vegetative) uprights was due to differences in upright growth resulting in increased inter-leaf shading on the upright since neither upright length (C.J. DeMoranville, unpublished data) nor leaf area per upright (J.E. Vanden Heuvel, unpublished data) differ between fruiting and vegetative field-grown ‘Stevens’ uprights.

Fruiting did not significantly effect carbohydrate concentrations or partitioning between soluble carbohydrates and starch (Fig. 3). In contrast, Hagidimitriou and Roper (1994) reported that TNSC was higher in vegetative than fruiting uprights, and attributed this to greater depletion of starch after flowering. Their work showed a late-season accumulation of soluble sugars in vegetative uprights. Differences between our observations and those of Hagidimitriou and Roper (1994) may be due to the small sink size (i.e., one fruit per fruiting upright) in our study.

Analysis of both upright and root samples for total N at fruit maturity did not reveal any significant differences that could explain the lower NCER of fruiting uprights. N concentration of the uprights was 0.51% and 0.55% for fruiting and vegetative uprights, respectively (Table 1). Hagidimitriou (1993) determined that fruiting uprights had greater N concentrations during flowering, but then did not differ from vegetative uprights following bloom. Fruiting uprights have previously been reported to have lower concentrations of N throughout the later portion of the season compared with vegetative uprights (DeMoranville, 1992; Eck, 1971). Lower N in fruiting uprights likely reduces NCER. Although there was no difference between the C:N ratio or N concentration between vegetative and fruiting uprights, there were differences between roots and uprights which changed with time of season. N concentration in both upright and root tissue decreased with time of season, however the magnitude of change was lower in root than upright tissue (Table 1). By maturity, upright tissue N concentration was about one-half of the concentration considered adequate (Davenport et al., 1995). The C:N ratio increased in all tissues with maturity, in part a reflection of the decrease in tissue N concentration. The C to N ratio was higher in root tissue than upright tissue prebloom but higher in uprights than roots at the other two growth stages and, like tissue N concentration, the magnitude of change was higher in upright than root tissue.

Defoliation did not significantly affect carbohydrate production or partitioning to root tissues at fruit maturity. The TNSC of root tissue before harvest was 1.6 to 1.9 mg/100 mg. Values of NCER reported here are consistent with those reported for current-year leaves of ‘Stevens’ (1.0 to 5.5 mmol·m⁻²·s⁻¹) by Hagidimitriou and Roper (1995) and lower than early morning values (10.5 to 12.5 mmol·m⁻²·s⁻¹) reported for runner leaves of the same cultivar by Kumudini (2004). The results of Kumudini (2004) are difficult to interpret as the leaves were borne on runners and were unlikely to have a strong sink demand (Roper and Klueh, 1996). In addition, Kumudini (2004) measured NCER of two leaves, while our work and that of Hagidimitriou and Roper (1995) are based on analysis of about 10-cm-long shoot segments.

Shading along the upright likely partially accounts for the lower values of NCER reported here compared to data for single leaves (Kumudini, 2004). Field-grown ‘Stevens’ vines operate at about 90% of maximum NCER at 700 µmol·m⁻²·s⁻¹ PPF (Hagidimitriou, 1993). According to Fig. 1, at 700 µmol·m⁻²·s⁻¹ PPF the fruiting uprights were at about 97% of maximum NCER, while the vegetative uprights were at about 82% of maximum NCER. Individual leaves at 15 to 25 °C saturate at 800 µmol·m⁻²·s⁻¹, while at higher temperatures (≥30 °C) leaves saturate at a lower irradiance of about 600 µmol·m⁻²·s⁻¹ (Kumudini, 2004). Since NCER was not affected by partial defoliation on any of the measurement dates when pre- and postdefoliation was compared, it is unlikely that improved light interception by remaining leaves affected NCER. However, gₖ may have been affected by leaf shading on the upright. The effect of fruiting on TNSC concentration in uprights and roots of field-grown cranberry may not be accurately reflected here, as uprights and roots from the whole vine (as opposed to a single upright) were collected to ensure adequate sample for HPLC analysis. However, in a production environment the distribution of uprights is roughly 50% each fruiting and vegetative uprights (Strik et al., 1991), and therefore our observations may reflect what occurs at the whole-vine level.

This study suggests the existence of a sink-limitation to carbon production early in the season in uprights with only one fruit. Following bloom, carbon production in uprights appears to be source-limited through to fruit maturity. Source limitations demonstrated by upright leaves may be able to be addressed through production practices which encourage upright elongation (such as appropriate nutrition and water management regimes), as long as increased vegetative growth is not at the cost of fruit growth. This work provides valuable insights into source–sink relationships in cranberry by presenting the first quantifications of the effects of partial defoliation on carbon production and partitioning by fruiting and vegetative cranberry uprights. The use of greenhouse vines, however, simplifies the relationships between multiple sinks that are present in the field. Sink activity may be stimulated by cultural practices such as irrigation and fertilization, as well as failure to protect vines from pests and diseases. These changing conditions underscore the need for further research into sink–source relationships of field-grown vines to improve our understanding of the effects of cultural practices on dry-matter production and allocation in this crop.

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