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Dry matter partitioning and photosynthetic response to biennial bearing and freeze damage in 'Empire' apple☆

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ABSTRACT

Biennial cropping is typically characterized as having 'ON' and 'OFF' years in which the 'ON' year produces an excessive crop load and the 'OFF' year has a very small crop load. Frost damage during the bloom period or winter freeze damage is another means of reducing the crop load that can initiate biennial bearing in an otherwise consistent cropping system. The objectives were to determine what effect single and multiple year crop loss had on the current and subsequent year's dry matter partitioning and photosynthesis. Dry matter partitioning and whole tree photosynthesis (A) were being measured in biennial bearing 'Empire' apple trees when 2 consecutive frosts occurred following an 'OFF' year. This provided an opportunity to evaluate two cycles of conventional biennial bearing and the effect of 3 years of suppressed crop load on dry matter partitioning and whole tree photosynthesis. Frost events reduced fruit dry weight to levels equivalent to the 'OFF' years but the 'SUPPRESSED' years (1 'OFF' and 1 or 2 frost years) reduced partitioning to wood dry matter and leaf + fruit more than the 'OFF' years while increasing the fruit dry matter partitioning compared to the 'OFF' years despite similar fruit yield and crop load. The 'ON' years had the highest fruit dry weight and% dry weight partitioned to fruit and leaf + fruit. Conversely, the 'ON' year had the least leaf area index (LAI) and% dry weight partitioned to wood and leaf tissue. There were no differences in canopy area, however, the 'ON' years had a significantly reduced LAI. Radiation use efficiency RUE; Annual biomass (kg)/PAR [(MegaMoles/growing season) × canopy area (m^2)] was linearly correlated with the% dry mass partitioned to fruit and negatively correlated with LAI. For a specified LAI, the 'ON' year had a greater RUE than the 'OFF' or 'SUPPRESSED' years and there were no differences between 'OFF' and 'SUPPRESSED' years. Analysis of daily photosynthesis (A) indicated that all three treatments were significantly different. The 'ON' years had the highest mean daily A (3.8 μmol/m^2/s), 'SUPPRESSED' years were intermediate (3.0 μmol/m^2/s) and the 'OFF' years had the lowest A (2.5 μmol/m^2/s). It appears that in years when fruiting is suppressed more than a single year, dry matter partitioning to wood is also suppressed and a great partitioning occurs to the remaining fruit and leaf tissue. This may be a response to a continued deficit of the hormonal complex supplied by fruit as they develop.

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1. Introduction

Biennial or alternate bearing in apple is a well documented sink-source interaction (Dennis, 2000; Goldschmidt, 2013; Jonkers, 1979; Lauri et al., 2014; Monselise and Goldschmidt, 1982). Hypotheses to explain the adverse effect of an excessive crop load on the subsequent years flower crop include hormonal signals (Guitton et al., 2012; Krasniqi et al., 2013; Pellerin et al., 2012; Saa and Brown, 2014), classical sink-source competition (Bruchou and Genard, 1999; Palmer et al., 1991) and interactions of hormonal signals with sink-source competition (Smith and Samach, 2013; Untiedt and Blanke, 2001). The apple crop load is managed in commercial production to ensure optimal fruit size and color using chemical agents that damage the flower causing it to later abort or hormonal agents that affect early fruit development (Dennis, 1979). Frost damage during the bloom period or winter freeze damage are another means of reducing the crop load that can initiate biennial bearing in an otherwise consistent cropping system resulting in a heavy crop load the year following the frost (Baraer et al., 2010; Nybom, 1992; Pramsohler et al., 2012).

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Biennial cropping is typically characterized as having 'ON' and 'OFF' years in which the 'ON' year produces an excessive crop load and the 'OFF' year has a very small crop load. The 'ON' year is characterized as having higher dry matter production, greater fruit number but lower fruit size and color and reduced shoot, leaf and secondary wood growth while the 'OFF' year has reduced overall dry matter production with increased shoot, leaf and wood growth and reduced fruit number but increased fruit size (Embree and Myra, 2007; Palmer, 1992; Palmer et al., 1991; Wibbe et al., 1994). The presence of fruit also increased leaf photosynthesis (*A*) while the absence of fruit reduced *A* (Duan et al., 2008; Gucci et al., 1991, 1995; Palmer et al., 1991; Wibbe et al., 1994; Wűnsche et al., 2000, 2005).

The present study was an opportunity to determine what effect multiple year crop loss has on the subsequent year's dry matter partitioning and photosynthesis. Dry matter partitioning and whole tree photosynthesis were being measured in biennial bearing 'Empire' apple trees when 2 consecutive frosts occurred following an 'OFF' year. This provided an opportunity to measure the suppressed crop load effects on dry matter production and photosynthesis and the effect on the subsequent 'ON' year.

2. Methods and materials

The apple orchard was a moderate density planting (500 ha^{-1}; 6.1 m × 3.3 m spacing) of 'Empire'/'Malling7A' planted in 1992 at the USDA/ARS Appalachian Fruit Research Station, Kearneysville, WV. All trees were sprayed with conventional pesticides to protect from disease or insect damage. Conventional orchard practices were used in tree training, mowing, nutrition, and weed control. Trees were in a biennial pattern. The study was initiated in 2006 when the trees were in the 'OFF' cycle. Eight trees were selected and measured annually until 2012. The following measurements were collected: pre-harvest-whole tree photosynthesis (*A*); harvest-fruit number and fruit weight; leaf mass and weights of pruned shoots and stems (Wood). Trees were annually pruned to fit within the whole canopy gas exchange chambers. The canopy area was determined by measuring the within-row and between-row dimension of the canopy and calculating the product prior to dormant season pruning. On average, fruit dry weight (at 60 °C) was 17% fresh weight and wood dry weight (at 60 °C) was 40% pruned shoot and stem weight in the field. Following harvest, trees were covered with a netting to collect all leaves. Total leaf mass was measured after drying at 60 °C. Tree leaf area was determined from the ratio of a ~50 leaf subsample leaf mass/leaf area ratio that was extrapolated to the total dry leaf mass.

Whole tree gas exchange was measured in open-top chambers similar to Glenn (2010). The whole canopy chamber was constructed of 0.762-mm-thick polycarbonate (Makrolon GP; Sheffield Plastics Inc., Bayer Material Sciences Pittsburgh, PA) in a rigid cube 2.4 × 2.4 × 2.4 m. A framed polycarbonate pitched roof covered the cube and the floor was a polyethylene tarp material split to the center to slide onto the tree and was sealed with a Velcro strip. Air was forced into each chamber with a one horsepower fan attached to a metal conduit with a cross-sectional area of 777 cm^2. Five holes were drilled in the conduit to measure air velocity with a velometer (Model 8346, TSI Inc., Shoreview, MN) and 10 2.5 cm positions at each sample port were measured at the beginning and end of the sampling period. Velocity data were averaged to calculate mass air flux. Air was forced into the chamber from below the chamber through a diffusion grate located 50 cm from the tree trunk. Leaf movement was visually assessed to insure no large eddies developed in the chamber. Approximately 6 chamber volumes were exchanged per minute and this air flow maintained internal air temperature 1–2 °C above ambient. Air temperature was measured with a shielded thermocouple hanging approximately 30 cm into the chamber through the outlet port. Whole canopy net CO_2 and H_2O exchange were measured with an infrared gas analyzer (IRGA) (CIRAS-1, PP Systems, Haverhill, MA) from the difference in CO_2 and H_2O concentration between the inlet (reference) and the outlet (analysis) ports of each chamber. Equal lengths of tubing were inserted into the conduit and the outlet port, and the sampled air was drawn to the IRGA with a pump. Response time was 5–10 s. The sampled air was blown into a cylinder that was sampled by the IRGA with its own sampling pumps. Multiple chambers were sampled sequentially at 5 min intervals using a programmable controller (SDM-CD16AC, Campbell Scientific, Logan, UT) that controlled solenoid valves on the reference and analysis tubes of each chamber. The controller was programmed and data collected with a datalogger (CR-7, Campbell Scientific).

Diurnal gas exchange data were collected: 2006 DOY's 217–225; 2007 DOY's 255–263; 2008 DOY's 238–244; 2009 DOY's 225–239; 2010 DOY's 241–242 and 264–266; 2011 DOY's 236–241; 2012 DOY's 217–225. During each sampling, four trees were simultaneously measured for multiple days. The chambers were moved to four other trees providing eight single tree replications of whole tree gas exchange. Photosynthetically active radiation (PAR), relative humidity, wind speed, pan evaporation, and air temperature were measured at a weather station approximately 500 m from the measurement site. Data were collected for 24 h each day but only data from 1000 to 1600 h, were analyzed and accumulated to derive daily *A*.

Each year was characterized as 'ON', 'OFF' or 'SUPPRESSED'. The 'SUPPRESSED' years (2009 and 2010) followed 'OFF' years and had frost events that reduced the flower numbers. Treatment effects were analyzed using repeated measures analysis of variance. Treatment means were compared using Fisher's protected least significant difference (LSD), $P \leq 0.05$.

Daily *A* was fitted to a multiple regression for all treatments and sampling dates over the 7 year period using the accumulated daily PAR, mean daily vapor pressure deficit (VPD), fruit dry weight, leaf area index (LAI) and leaf area.

Radiation use efficiency (RUE; annual biomass (kg)/PAR [(MegaMoles/growing season) × canopy area (m^2)]) was calculated for the growing season (May–September) using the measured dry weight of leaves, fruit and wood as annual biomass.

Analysis of covariance was used to test and separate treatment responses. Data were analyzed using SAS (version 8). Adjusted treatment means were compared using PDIFF, $P \leq 0.05$, which compares least squares means from the analysis of covariance.

3. Results and discussion

Two cycles of biennial bearing (2007–2008 and 2011–2012) follow expected patterns in which fruit dry mass in the 'ON' year (2007 and 2011) is greater than in the 'OFF' year (2008 and 2012) (Fig. 1). Apple response to frost damage is similar to the 'OFF' year with the reduction of the flower crop. Frost events in 2009 and 2010 reduced fruit dry weight to levels equivalent to the 'OFF' years (Fig. 1 and Table 1) but the 'SUPPRESSED' years reduced wood dry matter partition and leaf + fruit more than the 'OFF' years while increasing the fruit dry matter partitioning compared to the 'OFF' years despite similar fruit yield and crop load. Dry matter partitioning to wood decreased with each subsequent year that fruiting was suppressed by frost (Fig. 1) The 'ON' years had the highest fruit dry weight and% dry weight partitioned to fruit and leaf + fruit. Conversely, the 'ON' year had the least leaf area index and% dry weight partitioned to wood and leaf tissue.

There were no differences in canopy area, primarily because the trees were dormant pruned to fit within the whole canopy gas

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