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Onions Selected for Reduced Symptom Expression of Iris Yellow Spot Have Higher Photosynthetic Rates

Joseph B. Wood and Christopher S. Cramer
Department of Plant and Environmental Sciences, New Mexico State University, Las Cruces, NM 88003, USA

Robert Steiner
Department of Economics, Applied Statistics, and International Business, New Mexico State University, Las Cruces, NM 88003, USA

Richard Heerema
Department of Extension Plant Sciences, New Mexico State University, Las Cruces, NM 88003, USA

Brian J. Schutte
Department of Entomology, Plant Pathology, and Weed Science, New Mexico State University, Las Cruces, NM 88003, USA

Ivette Guzman
Department of Plant and Environmental Sciences, New Mexico State University, Las Cruces, NM 88003, USA

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Abstract. **Bulb onion (*Allium cepa* L.) is an economically valuable vegetable crop in the United States. Onion production is threatened by onion thrips, which are the vector for *Iris yellow spot virus*, which is the causal agent of Iris yellow spot (IYS). New Mexico State University (NMSU) breeding lines 12-236, 12-238, 12-243, and 12-337 have exhibited fewer IYS disease symptoms in the field; however, little is known about the effects of the disease on the photosynthesis rate (P_n). We hypothesized that these NMSU breeding lines would have a higher P_n than IYS-susceptible cultivars Rumba and Stockton Early Yellow. To test this hypothesis, a field study was conducted for 3 years at NMSU, and P_n was measured five times throughout each season at 2-week intervals. During bulb development and maturation, which occurred at 10 and 12 weeks after transplanting, all NMSU breeding lines exhibited a higher P_n when compared with that of an IYS-susceptible cultivar. P_n was highest at the end of the vegetative growth stage and decreased as bulbs approached maturation for all cultivars. Additionally, a high P_n at 10 and 12 weeks after transplanting coincided with high bulb weight at harvest. NMSU breeding lines have increased P_n compared with that of IYS-susceptible cultivars and resulted in larger and more marketable bulbs. These results indicate that maintaining P_n may be related to reduced IYS symptom expression of onion.**

Bulb onion (*Allium cepa* L.) is an economically valuable vegetable crop in the United States. Approximately 34,000 metric tons of onions, valued at $877.8 million, were harvested in the United States in 2020 (US Department of Agriculture, National Agricultural Statistics Service 2021). Many pests and diseases plague onion production, but Iris yellow spot (IYS), which is caused by *Iris yellow spot virus* (IYSV), has been identified as a major cause of economic loss. IYSV is in the genus *Tospovirus*, family *Bunyaviridae*, and is present in most regions of the world that produce *Allium* sp. (Bag et al. 2015). The pathogen has a wide host range and can infect many cultivated and wild *Allium* species such as onion, garlic (*Allium sativum* L.), chives (*Allium schoenoprasum* L.), and shallots (*Allium cepa* var. *aggregatum L.*).

Onion thrips (*Thrips tabaci* L.) are the primary vector for IYS in onions and are increasingly difficult to control because of pesticide resistance (Rosen et al. 2021). These insects cause a substantial amount of physical damage and, when compounded with the stress caused by the virus, can prove detrimental to an onion plant (Gent et al. 2006). Along with the loss of the photosynthetic area, biotic stressors are known to create source–sink imbalances that can inhibit gene expression related to the production of chloroplast protein complexes, which can have a lasting negative effect on the photosynthesis rate (P_n) (Balachandran et al. 1997). This loss of the photosynthetic area and chloroplast function may result in reduced onion bulb size and yield losses of more than 50% (Diaz-Montano et al. 2011).

P_n is important during bulb maturation because, during this period, the plant is storing carbohydrates that will be used for growth after dormancy (Brewster 2008). Reduced P_n during bulb maturation can lead to decreased stored carbohydrates, reduced bulb size, and increased sprouting during storage (Pak et al. 1995). To track bulb initiation and maturation, bulb diameter and sheath diameter can be combined to create an index of bulb development called the "bulbing ratio" (Brewster 1982; Lancaster et al. 1996). The bulbing ratio is used as an index of bulb development, and a ratio of more than two indicates the initiation of bulb development (Ikeda et al. 2020). Bulb initiation coincides with the development of fleshy basal leaves and a reduction in green leaf development (Brewster 2008). This causes the bulb to swell faster than the neck, thus increasing the bulbing ratio. To measure the bulbing ratio, the onion must be removed from the ground so that the bulb as well as the neck can be measured. However, the neck can be measured nondestructively, and this alone can be used to track the onion bulb development (Nourbakhsh and Cramer 2022). By exploring the relationship between the sheath diameter and P_n, it may be possible to determine whether P_n can be used to predict the bulb size and crop maturity.

For the past 10 years, the onion breeding program at New Mexico State University (NMSU) has been selecting onion germplasm for reduced IYS symptom expression (Cramer et al. 2012, 2014, 2017; Mohseni-Moghadam et al. 2011; Multani et al. 2009). This research has resulted in plants exhibiting 30% to 67% less IYS symptoms than an IYS-susceptible cultivar and unselected germplasm from the same breeding lines (Cramer et al. 2014). Mechanisms associated with the reduction in IYS symptom expression in onion are poorly understood. Understanding these mechanisms will allow for more informed decisions during selection, resulting in onion germplasm with increased resistance to IYS.

To further characterize breeding lines selected for decreased IYS symptom expression, a field study was conducted for 3 years. We hypothesized that breeding lines selected for decreased IYS symptom expression maintain higher P_n after IYSV infection. We also hypothesized that P_n would decrease as bulbs matured. The objectives of this study were to compare the P_n during bulb maturation between

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I.G. is the corresponding author. E-mail: ivguzman@nmsu.edu.
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NMSU breeding lines with reduced IYS disease symptoms and IYS-susceptible cultivars and to assess changes over time in P_n for NMSU breeding lines with reduced IYS disease symptoms.

Materials and Methods

Onion germplasm. Breeding lines NMSU 12-236, 12-238, 12-243, and 12-337 were developed previously for reduced IYS symptom expression (Kamal et al. 2021). Plants of these lines were evaluated in 2019, 2020, and 2021, along with an IYS-susceptible cultivar Rumba (2019) or the cultivar Stockton Early Yellow (2020, 2021). 'Stockton Early Yellow' was used in 2020 and 2021 because seeds of 'Rumba' stopped being produced. The seeds of all entries were sown in a greenhouse in early January in 10-cm-deep plastic flats filled with MetroMix360 (SunGro, Bellevue, WA) potting mix. Seedlings were transplanted to the field in March, when seedlings had reached the four- to five-leaf stage.

Field design. This study was conducted in Las Cruces, NM, at the Fabian Garcia Science Center of NMSU (lat. 32.279°N, long. 106.778°W) in 2019 and 2020, and at the Leyendecker Plant Science Research Center of NMSU (lat. 32.198°N, long. 106.748°W) in 2021. In 2019, the soil type where the study was located was a Glendale loam and Brazito very fine sandy loam. In 2020, the soil type was a Harkey clay loam. In 2021, the soil type was a Brazito very fine sandy loam. The field was arranged using a randomized complete block design with three blocks and four replications per block. Each replication included all five onion entries. Experimental units (herein referred to as "plots") were 3.3-m-long sections of raised bed with two rows of onion of a specific line planted 7 to 8 cm apart. Plots were spaced 0.5 m apart. From each plot, five onion plants in 2019 and three onion plants in 2020 and 2021 were arbitrarily chosen to be sampled repeatedly throughout the season.

To ensure disease pressure was established throughout the field, viruliferous thrips-infested bulbs (herein referred to as "infected onions") from the previous year were sown around the perimeter of each replication, thus establishing a source of disease. These bulbs were sown in the fall (Oct 2018, Oct 2019, and Nov 2020) before the spring during which the onion entries were transplanted. This field layout allowed the bulbs to sprout and produce established plants before overwintering in the field. Between the infected onions and the onion entries, a bed was seeded with the onion cultivar NuMex Freedom at the same time as the planting of the infected onion bulbs. This experimental design was previously used to create uniform disease pressure throughout an onion field (Cramer et al. 2012, 2014, 2017; Mohseni-Moghadam et al. 2011). All irrigation was performed using a subsurface drip irrigation system installed in the field before bulbs were sown in the fall. The onions were grown using standard cultural practices for growing onions in southern New Mexico (Walker et al. 2009). Insecticides were not applied to preserve the population of thrips.

Photosynthetic measurements. Each plant selected for photosynthetic measurements was evaluated every 2 weeks starting at 8 weeks and concluded at 15 weeks after transplanting. Henceforth, biweekly evaluations are referenced as sequential sampling events 1 through 5. These sampling events occurred during the bulb initiation stage through the bulb maturation stage in 2019 and 2020. Because of poor stand establishment in 2021, onions were replanted, and sampling events occurred during the vegetative growth stage through the bulb maturation stage. For each sampling event, we used portable photosynthesis systems with 6-cm^2 chambers (LI-6400XT in 2019 and LI-6800 in 2020 and 2021; LI-COR Inc., Lincoln, NE) to measure P_n.

P_n was measured in the field by clamping the portable photosynthesis system leaf chamber onto an onion leaf and waiting for gas exchange parameters to stabilize before performing the measurement. Inside the chamber, photosynthetically active radiation was maintained at 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ because it was predetermined by measuring the light intensity in the field at the time of sampling. The reference carbon dioxide concentration was maintained at 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ because this is near the atmospheric carbon dioxide concentration (Zheng et al. 2019). The leaf was kept in the chamber for no more than 1 min per measurement. Gas exchange parameters were measured using the second or third newest onion leaf 10 to 15 cm away from the base of the onion plant. Leaf width was also recorded because onion leaves did not fill the LI-6800 or the LI-6400XT leaf chamber. This was performed using a scale to measure the leaf width (cm) at the point where the leaf entered the chamber. For the LI-6400XT, leaf widths were used to calculate total leaf area in the raw data spreadsheet. For the LI-6800, leaf width was entered under the "constants" tab, which automatically adjusted the carbon assimilation rate measurement for the area of the onion leaf in the chamber. Samples were obtained between 10:00 AM and 12:00 PM. This time frame coincided with the daily maximum photosynthetic rates as determined from the P_n diurnal response curves (data not shown). Data were collected every 2 weeks regardless of the irrigation event; however, irrigation events were based on the managed allowed depletion (MAD), which did not surpass 30%; therefore, plants were not drought-stressed (Walker et al. 2009). The MAD was calculated as follows:

$$MAD = \sum_{i=1}^{d} (Daily\ ET * Crop\ coefficient) - \text{Precipitation}$$

Bulb weight and sheath diameter. The sheath diameter (mm) was measured using calipers at the point just above where the neck meets the bulb. Measurements of plants of onion entries were obtained at each sampling event except for sampling event 4 in 2021 because of heavy rains. Bulbs were hand-harvested at the end of the season, and leaves and roots were removed. Plants were considered mature when 80% had lodged and the necks had softened. Each bulb was weighed individually using a scale.

Statistical analysis. Years were analyzed separately because of to differences in soil type and weather conditions in each year when the experiment was conducted. Within years, the mean P_n from 10 to 12 weeks after transplanting was analyzed to target the bulb maturation stage of growth. To determine if the breeding line affected P_n, data were analyzed with linear mixed effects models. Fixed effects were entries and random effects included the block and subsample. The F-protected least significant difference was used to detect differences between entries. The Pearson correlation test was used to determine if there was a correlation between the P_n and sheath diameter. Data were analyzed using SAS OnDemand (SAS® Studio 3.8, 2021), and significance was defined as $\alpha > 0.05$.

Results

Plants from breeding lines selected for reduced IYS symptom expression had a higher P_n than plants of the IYS-susceptible onion cultivars Rumba and Stockton Early Yellow at the bulb maturation growth stage in 2019 and 2020, respectively (Table 1). In 2021, NMSU 12-238 had a higher P_n than 'Stockton Early Yellow'. The breeding line with the highest P_n was 12-243, with 27.19 ± 2.68 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in 2020, and the susceptible cultivar with the lowest P_n was 'Rumba', with 8.95 ± 0.85 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in 2019 (Table 1). These differences were most pronounced at sampling events 2 and 3, when plants were in the bulb development growth stage (Table 1 and Figs. 1 and 2). P_n decreased as onion plants approached maturity in 2019 and 2020 (Fig. 1). For all entries, P_n was highest at the beginning of the bulb initiation growth stage, and it decreased as bulb size increased and plants approached maturation.

Compared with the IYS-susceptible cultivars, breeding lines selected for reduced IYS symptom expression had greater bulb size than the susceptible cultivar, except in 2021, when bulb size did not differ between 12-236 and 'Stockton Early Yellow' (Table 1). Breeding lines 12-243, 12-337, and 12-238 had the highest P_n and greatest bulb size across years and sampling events. No differences were observed between these lines in 2019 and 2020; however, breeding line 12-337 was greater than 12-238 in 2021.

P_n decreased from sampling event 2 to to sampling event 4 for all breeding lines, whereas onion plants continued to produce leaf scales that increased the bulb size and sheath diameter (Fig. 1). No correlation was found between the P_n and sheath diameter. However, in 2019 and 2020, at sampling events 2 and 3, the sheath diameter increased while the P_n decreased. The sheath diameter decreased at sampling events 4

Table 1. Annual average net photosynthesis by line at sampling events 2 and 3 during bulb maturation and bulb weight at harvest.

Yr	Line	Net photosynthesis ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Bulb wt (g)
2019	'Rumba'	08.95 ± 0.85 b	102.93 ± 11.2 b
	12-236	15.30 ± 1.05 a	186.12 ± 11.2 a
	12-238	14.55 ± 1.34 a	207.14 ± 11.2 a
	12-243	14.61 ± 1.00 a	198.78 ± 11.2 a
	12-337	14.75 ± 1.24 a	223.89 ± 11.2 a
2020	'Stockton Early Yellow'	21.58 ± 0.89 b	95.37 ± 12.0 b
	12-236	26.39 ± 1.35 a	173.97 ± 12.0 a
	12-238	24.10 ± 1.52 a	234.19 ± 12.0 a
	12-243	27.19 ± 2.68 a	201.82 ± 12.0 a
	12-337	25.98 ± 2.04 a	194.27 ± 12.0 a
2021	'Stockton Early Yellow'	20.91 ± 1.64 b	82.82 ± 11.9 c
	12-236	23.51 ± 1.91 ab	60.74 ± 11.3 c
	12-238	26.29 ± 1.62 a	101.66 ± 11.3 b
	12-243	23.47 ± 1.77 ab	160.30 ± 11.9 a
	12-337	22.97 ± 1.84 b	170.19 ± 10.8 a

Cultivar comparisons were performed by year and sampling event. Different letters represent differences between means as determined by Fisher's least significant difference with $\alpha = 0.05$. Rumba and Stockton Early Yellow are susceptible cultivars. All other breeding lines have been previously selected for decreased Iris yellow spot symptom expression.

and 5 because, at maturation, parenchyma cells in the neck begin to break down (Rahim and Fordham 1988). This resulted in less resistance to the caliper when a measurement was performed.

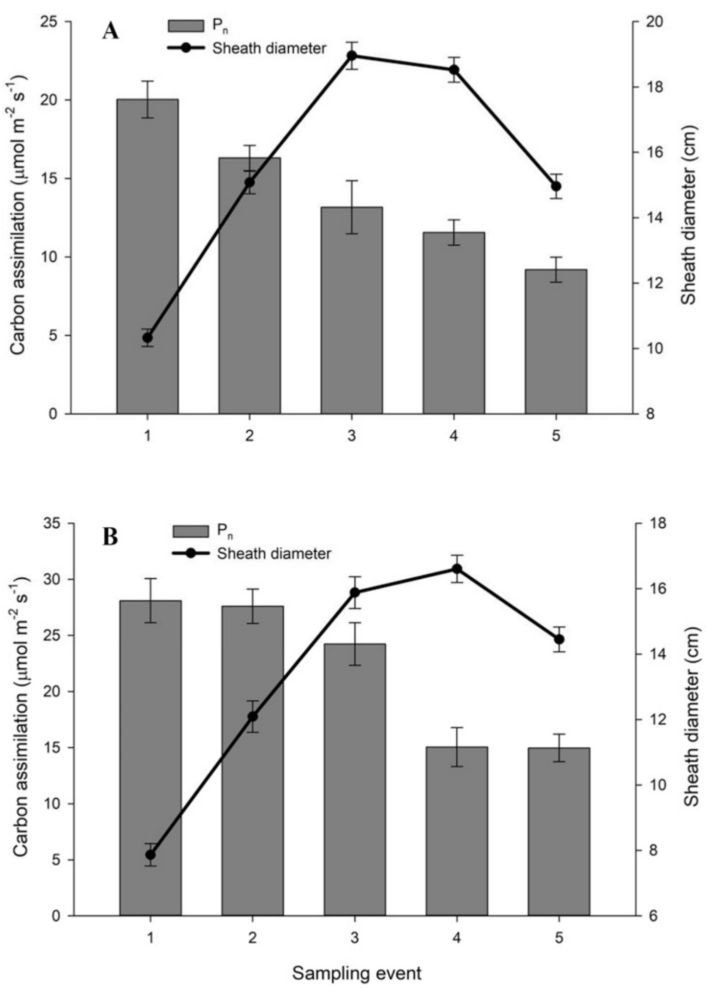

Fig. 1. Mean photosynthesis rate and sheath diameter of New Mexico State University onion breeding lines grown in (**A**) 2019 and (**B**) 2020 in southern New Mexico. The sampling event refers to evaluations every 2 weeks starting at 8 weeks and concluding at 16 weeks after transplanting.

Discussion

In this study we used a portable photosynthesis meter to measure the P_n of four NMSU breeding lines selected for reduced IYS symptom expression as well as two IYS-susceptible cultivars. We focused on P_n during bulb maturation because P_n during this period influences bulb size and storage potential (Pak et al. 1995).

No differences in P_n were observed between NMSU breeding lines in 2019 and 2020; however, some differences were seen in 2021. This was likely because of adverse environmental conditions, including insect and weed pest pressure, in 2021, which prevented some plots from becoming fully established early in the season. Additionally, heavy rain events occurred in the final weeks of maturation. Breeding lines 12-236 and 12-238 were most affected by these setbacks, which may explain the differences seen in 2021.

Data collected during this experiment suggest that breeding lines selected for reduced IYS symptom expression can tolerate stress caused by thrip damage and IYS infection, with a higher P_n resulting in a larger onion bulb compared with IYS-susceptible onion cultivars. However, differences in P_n among onion entries in the field can be partially attributed to how well the different entries avoided onion thrip damage and IYSV. Research has indicated that thrip avoidance is associated with leaf color because this plant characteristic influences onion thrip attraction to onion plants (Allan and Gillett-Kaufman 2018). Leaf color is affected by the composition of the epicuticular waxes, which can range from waxy to semi-glossy and glossy. The NMSU breeding lines in this experiment had semi-glossy and glossy leaves, whereas the susceptible cultivars Rumba and Stockton Early Yellow had waxy leaves (Nourbakhsh and Cramer 2022). The epicuticular wax compositions of 'Rumba' and 'Stockton Early Yellow' make them more attractive to onion thrips, which increases the thrip population densities and thrip damage to leaves (Kamal et al. 2021). This was true in this experiment because higher symptom expression and thrip damage were observed on 'Rumba' and 'Stockton Early Yellow' plants than on the NMSU breeding lines. This damage occurs early in the season and may increase disease incidence and severity as well as affect P_n during the bulb development growth stage. Reduced symptoms may be associated with higher P_n because there is less damaged tissue; therefore, breeding for reduced symptom expression may allow for higher P_n.

Additionally, there may be differences in the photosynthetic capacity or maximum photosynthetic rate between plants of different entries in the absence of biotic stress. A carbon dioxide response curve could provide information about carboxylation efficiency, stomatal limitations, and carboxylation limitations, all of which reflect the maximum photosynthetic performance of a plant (Manter and Kerrigan 2004). The maximum carbon assimilation rate recorded in the response curve would indicate how efficiently a cultivar is assimilating carbon when the stomatal and carbon limitations are removed (Stinziano et al. 2017). These parameters are increasingly relevant as changes in atmospheric carbon dioxide

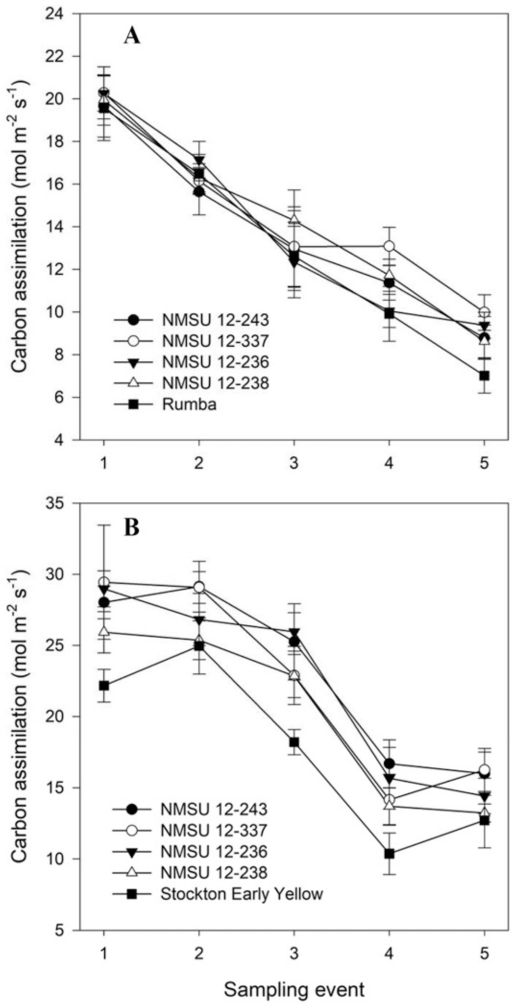

Fig. 2. Photosynthesis rates for New Mexico State University onion breeding lines and Iris yellow spot (IYS)-susceptible cultivars grown in (**A**) 2019 and (**B**) 2020 in southern New Mexico. The IYS-susceptible cultivars used were Rumba in 2019 and Stockton Early Yellow in 2020.

drive climate change and affect how these plants are cultivated.

In our study, we found that as onion leaves senesce and the onion plant begins to mature, carbon assimilation decreases. During bulb maturation, leading up to dormancy, there is a sharp decline in cell division at the shoot apex (Pak et al. 1995). Plant dormancy is characterized by a decrease in mRNA needed to produce histone 2A, which is a protein that is incorporated in chromosomes at mitosis and associated with cell division (Carter et al. 1999). Accordingly, the onset of dormancy includes a reduction in mitotic index and suppression of cellular division (Brewster 2008). The results of this study suggest that suppressed cell division is preceded by a decline in P_n. When the plant begins to become dormant, abscisic acid (ABA) is translocated from the leaves to the bulb, and this ABA maintains dormancy in the bulb (Stow 1976). The accumulation of ABA in the leaves of the onion plant may also influence the reduction in P_n. If onion plants are stressed, then there may be an effect on ABA production and translocation that would impact the dormancy of the bulb. Stressed plants will be less likely to produce a marketable bulb before the onset of dormancy. The relationship between the accumulation of ABA and P_n in the presence of stress caused by IYSV could be an important topic for future research.

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