

Auxin Applications Affect Posttransplant CO₂ Exchange Rate and Growth of Bare-rooted Vinca [*Catharanthus roseus* (L.) G. Don] Seedlings

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ABSTRACT. Uprooting and transplanting seedlings can cause root damage, which may reduce water and nutrient uptake. Initiation of new roots and rapid elongation of existing roots may help minimize the negative effects of transplant shock. In this study, seedlings with four true leaves were transplanted into diatomaceous earth and the plants were transferred to a growth chamber, where they were treated with NAA (0, 0.025, 0.25, and 2.5 mg·L⁻¹; 36 mL/plant). The effects of drenches with various amounts of 1-naphthaleneacetic acid (NAA) on the posttransplant CO₂ exchange rate of vinca [*Catharanthus roseus* (L.) G. Don] were quantified. Whole-plant CO₂ exchange rate of the plants was measured once every 20 minutes for a 28 day period. Seedlings treated with 0.025 or 0.25 mg·L⁻¹ recovered from transplant shock more quickly than plants in the 0 and 2.5 mg·L⁻¹ treatments. Naphthaleneacetic acid drenches containing 0.025 or 0.25 mg·L⁻¹ increased whole-plant net photosynthesis (P_{net}) from 10 days, dark respiration (R_{dark}) from 12 days, and carbon use efficiency (CUE) from 11 days after transplanting until the end of the experiment. The increase in CUE seems to have been the result of the larger size of the plants in these two treatments, and thus an indirect effect of the NAA applications. These differences in CO₂ metabolism among the treatments resulted in a 46% dry mass increase in the 0.025 mg·L⁻¹ treatment compared to the control, but shoot-root ratio was not affected. The highest rate of NAA (2.5 mg·L⁻¹) was slightly phytotoxic and reduced the growth rate of the plants.

Root damage caused by uprooting and transplanting can reduce the effective root area and limit the ability of plants to absorb water and nutrients (Kramer, 1983). Transplant shock can cause water stress (Berkowitz and Rabin, 1988) and decrease the nutrient uptake of plants (Bloom and Sukrapanna, 1990). Initiation of new roots and rapid elongation of existing roots into the surrounding soil may help plants to recover more quickly from the harmful effects of transplant shock.

Auxins are commonly used to stimulate root formation in plants (Blakely et al., 1988; Selby et al., 1992). However, literature reports on the biological effects of auxins appear to be contradictory. It has been reported that exogenous auxin applications inhibit root elongation of pea (*Pisum sativum* L.) (Eliasson et al., 1989) and corn (*Zea mays* L.) (Pilet and Saugy, 1987), while Lippmann et al. (1995) and Leinhos and Bergmann (1995) found that auxin-producing bacteria and auxin applications increased lateral root production and stimulated root elongation of corn. Exogenous auxin applications also increased the shoot growth (Lippmann et al., 1995) and the concentrations of Ca, K, Mg, P, Fe, and Zn in the roots of corn (Leinhos and Bergmann, 1995). These contrasting findings may be explained by the dose-dependent effect of auxins. Generally, auxins stimulate the initiation of new roots at relatively high concentrations, while root elongation is promoted by lower concentrations (Pierik, 1985).

Based on these findings, it appears that auxins may have the ability to stimulate root growth and possibly minimize transplant shock, if applied at a proper rate. Van Iersel (1998) indicated that applications of indole-3-acetic acid (IAA) and 1-naphthaleneacetic acid (NAA) to bare-rooted vinca transplants increased the

posttransplant growth of the plants. Percival and Gerritsen (1998) showed that auxin applications increased the root growth of several tree species after removal of half of the root system. However, both Percival and Gerritsen (1998) and van Iersel (1998) reported that high concentrations of auxins can be phytotoxic and cause plant death. In addition, Percival and Gerritsen (1998) showed that the reaction of trees to auxin drenches is species-dependent.

Although auxins appear to be beneficial in reducing the effects of transplant shock, there is no information on the basic processes that affect the growth of auxin-treated plants. The underlying hypothesis for this study was that auxins can have a stimulating effect on root initiation and/or elongation, which can help plants recover from transplant shock. Although there is no indication that NAA has a direct effect on photosynthesis or carbon accumulation of plants, it may have indirect effects as a growth stimulant. As with most hormonal responses, the effects are likely to be dose-dependent. Thus, the objective of this study was to quantify the effect of different rates of NAA on the whole-plant carbon exchange rate (CER) and growth rate of bare-rooted vinca transplants.

Carbon assimilation is the main process responsible for dry matter increases (growth) in plants (Lawlor, 1995). Therefore, if auxin applications stimulate posttransplant growth of seedlings, the response should be apparent in the photosynthetic and/or respiratory rate of the plants. Whole-plant CER measurements are particularly useful to determine effects on growth rate (Bugbee, 1992), since they provide a direct measure of the carbon accumulation by plants. Continuous CER measurements over a prolonged period (weeks) also make it possible to determine exactly at what time treatment effects occur. This type of information is difficult to determine with more traditional techniques like dry mass measurements. Vinca was used as a model species, because it has relatively slow root growth for a bedding plant (unpublished results) and growers have reported problems associated with poor posttransplant growth and small root systems of vinca (Thomas and Wade, 1997).

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Materials and Methods

PLANT MATERIAL. Vinca 'Cooler Peppermint' seeds were planted in a peat-based growing mix (Redi-Earth, The Scotts Co., Marysville, Ohio) and germinated in the dark at 20 °C. The seedlings were subsequently transferred to a double-layer polyethylene greenhouse and grown until the second pair of true leaves appeared. Temperature set points for the greenhouse were 23 (day) and 18 °C (night). The seedlings were then transplanted into cell packs (166 mL/cell) filled with diatomaceous earth (Isolite CG-2, Sundine Enterprises, Arvada, Colo.). During transplanting, most of the growing mix was removed from the root system by dipping the roots in water. The root systems were handled carefully and no visible root damage occurred during transplanting. However, it is likely that some injury to the fragile, small root hairs occurred. Diatomaceous earth was used as a posttransplant growing medium in this experiment, because it is easy to remove from the root system and thus facilitates accurate root size measurements. Diatomaceous earth is a chemically inert growing substrate consisting mainly of SiO₂ (78%), Al₂O₃ (12%), and Fe₂O₃ (5%), with a low cation exchange capacity (<0.02 meq·g⁻¹).

Eight groups of seedlings were placed in watertight trays (28 plants/tray) and transferred to transparent acrylic chambers (3.2 × 5 × 6 dm³), which were placed inside two larger growth chambers (model E-15; Conviron, Asheville, N.C.). Plants were watered as needed with a complete 20N-4.4P-16.6K water-soluble fertilizer (20-10-20 Peat-Lite Special, The Scotts Co.), containing 100 mg·L⁻¹ N. Environmental conditions inside the chambers were 22/18 °C day/night, with a 14-h light period and a photosynthetic photon flux of 425 μmol·m⁻²·s⁻¹ at the canopy level, which resulted in a total daily photon flux of 21.4 mol·m⁻². Relative humidity inside the acrylic chambers was ≈75% during the light period and 100% at night.

TREATMENTS. One day after transplanting (DAT), plants were treated with NAA solutions (0, 0.025, 0.25, and 2.5 mg·L⁻¹). The NAA was first dissolved in a small volume of ethanol and subsequently mixed with deionized water. One liter of NAA solution was applied to the trays (36 mL/plant) and absorbed by the diatomaceous earth through holes in the bottom of the pots. Thus, the auxin never was in contact with the shoots of the plants.

MEASUREMENTS. Whole-plant CER of the eight groups of plants was measured with a multi-chamber, open, CO₂ exchange system, designed following the principles outlined by Bugbee (1992). Ambient air was blown into the acrylic chambers and air flow was measured with mass flow meters (GFM37-32, Aalborg Instruments and Controls, Monsey, N.Y.). The difference in the CO₂ concentration of the air entering and exiting the chamber was measured with an infrared gas analyzer (LI-6251; LI-COR, Lincoln, Neb.). Whole chamber CER (μmol·s⁻¹) was calculated as the product of mass flow (mol·s⁻¹) and the difference in CO₂ concentration (μmol·mol⁻¹). Gas exchange data of every group of 28 plants was collected at 20-min intervals until 4 weeks after transplanting. Both net photosynthesis (P_{net}) and dark respiration (R_{dark}) data are reported as positive quantities, except for a brief period shortly after transplanting when P_{net} was actually negative. CO₂ exchange rates are expressed on a per plant basis, and are thus measures of plant growth rate.

Since whole plants, including the containers, were enclosed in the gas exchange chambers, CER measurements include growing medium and root respiration. Since root respiration is part of the whole-plant metabolism, this should be included in whole-plant CER measurements. Respiration by microorganisms in the root zone normally consists of two separate processes, namely respi-

ration of organic compounds leaking from plant roots and microbial breakdown of the growing medium. Respiration resulting from the breakdown of organic products leaking from plant roots should be included in whole-plant net CER measurements, since the carbon in these compounds was originally fixed in the photosynthetic process, but are no longer available for plant growth after they leak from the roots. Breakdown of organic matter in the growing medium by microorganisms can cause small errors in whole-plant CER estimates, but was not a factor in this experiment since plants were grown in diatomaceous earth, an inert substrate.

Cumulative carbon gain of the plants (CCG) at time t was calculated as the integral of the CO₂ exchange data and is an indicator of plant growth since the start of the experiment: $CCG_t = \int_0^t CER dt$, where t = time since the start of the experiment.

Although photosynthesis is often used as a measure of the

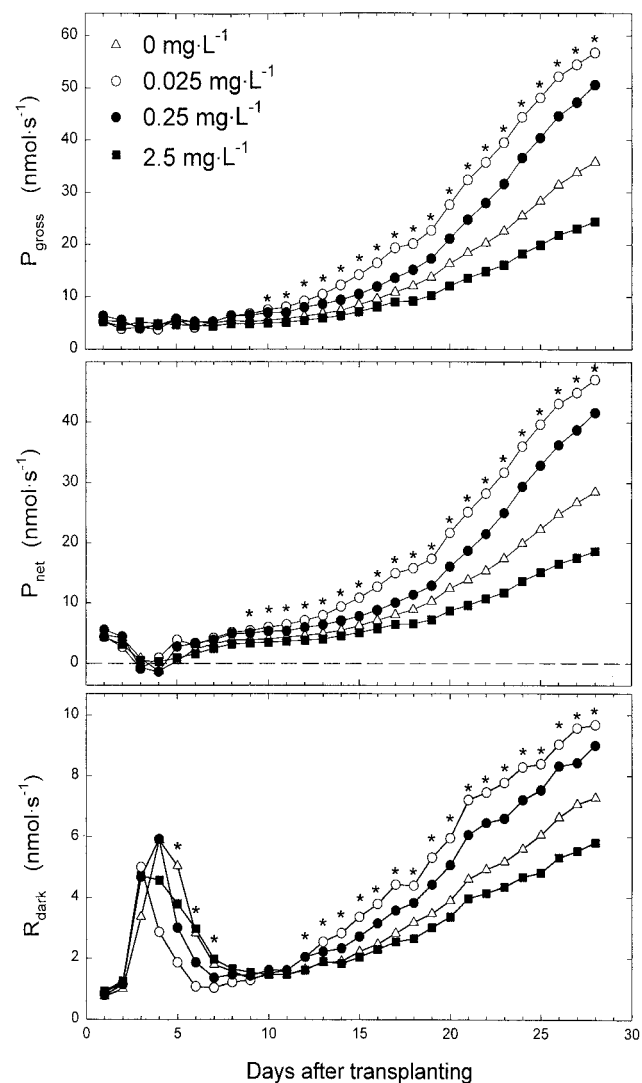


Fig. 1. The effect of exogenous auxin applications on the CO₂ exchange rates of vinca seedlings. Four different concentrations of NAA solutions were applied to the root zone of the plants (36 mL/plant) at one day after transplanting. Whole-plant nighttime respiration (R_{dark}) and daytime net photosynthesis (P_{net}) were measured semicontinuously and data points represent the average CO₂ exchange rate per plant. Gross photosynthesis (P_{gross}) was calculated as the sum of P_{net} and R_{dark} . Significant quadratic correlations between CO₂ exchange rate and NAA concentration are indicated by an asterisk ($P < 0.05$). The NAA concentration was transformed by $\log(\text{conc} + 0.0025)$ before regression.

growth rate of plants, growth also depends on the efficiency with which plants convert carbohydrates into dry matter. This can be estimated from P_{net} and R_{dark} measurements. Carbon use efficiency (CUE), the ratio between carbon incorporated in plant dry mass and the amount of carbon fixed in photosynthesis, was calculated as

$$\text{CUE} = (P_{\text{net}} \times t_l - R_{\text{dark}} \times t_d) / (P_{\text{gross}} \times t_l) \quad [1]$$

where P_{net} = average net photosynthesis during the light period, t_l = length of the light period (s), t_d = length of the dark period (s), R_{dark} = average respiration during the dark period, and, P_{gross} = average gross photosynthesis during the light period (estimated as the sum of P_{net} and R_{dark} , assuming equal respiration rates in the light and dark).

At the end of the experiment, leaf area of the plants was determined with a leaf area meter (LI-3100) and shoot and root dry mass were determined after drying the plant material in a forced-air oven at 70 °C.

EXPERIMENTAL DESIGN. The experiment was designed as a randomized complete block with repeated measures and two replications. The two growth chambers were used as experimental blocks and the experimental unit was a group of 28 plants. Daily averages of P_{net} and R_{dark} were calculated from the CER data and these values were used for data analysis. The data derived from the CER measurements (P_{net} , R_{dark} , P_{gross} , CUE) were analyzed separately for each day. Linear and quadratic curve fitting was used to describe the effect of NAA concentration on the response variables. NAA effects were considered to be significant at $P < 0.05$. Before regression analysis, NAA concentrations were transformed according to $\log(\text{conc} + 0.0025)$. CO_2 exchange and CUE data were normalized by dividing the data by the replication mean to account for differences between the two replications.

Results and Discussion

Whole-plant P_{net} of the plants in all treatments decreased during the first 3 to 4 DAT and increased thereafter (Fig. 1). This initial decrease in P_{net} was not caused by a reduction in the photosynthetic capacity of the plants, since the decline in P_{gross} during this period was negligible. The decrease in P_{net} was mainly caused by an increased R_{dark} . Dark respiration showed a fast increase immediately after transplant and reached a peak at 3 to 4 DAT (Fig. 1). This increase in R_{dark} probably was the result of transplant shock. Transplanting can contribute to plants stress and an increase in respiration is a normal response to environmental stress (Levitt, 1972). The increase in R_{dark} after transplanting may be a useful measure to quantify the severity of transplant shock.

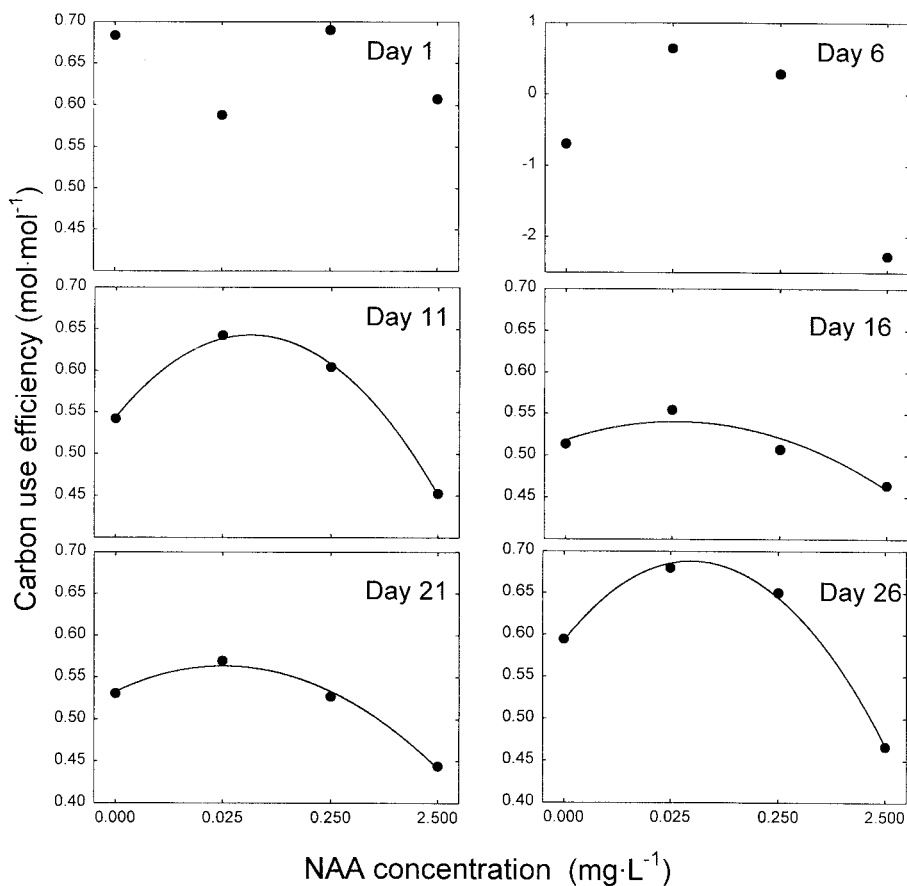
In all treatments, P_{net} and P_{gross} increased from 4 DAT until the end of the experiment. These increases in P_{net} are the result of an increase in leaf area, which allows the plants to intercept more of the available light. Initially, the increase in P_{net} was similar in all four treatments and there were no significant effects of the NAA treatments on P_{net} and P_{gross} during the first 8 d of the experiment (Fig. 1). After that, there were clear differences in photosynthesis among the treatments. Plants in the

0.025 mg·L⁻¹ treatment had the highest P_{net} and P_{gross} from 9 DAT until the end of the experiment, followed by the plants in the 0.25 mg·L⁻¹ treatment. The lowest P_{net} and P_{gross} occurred in the 2.5 mg·L⁻¹ treatment.

After the initial increase in R_{dark} , it decreased again (Fig. 1). This decrease in R_{dark} was different among the NAA treatments. The decrease was fastest in the 0.025 and 0.25 mg·L⁻¹ treatments. From 5 to 7 DAT, the plants treated with 0.025 and 0.25 mg·L⁻¹ NAA had a lower R_{dark} than the untreated control and the 2.5 mg·L⁻¹ treatment. This suggests that the 0.025 and 0.25 mg·L⁻¹ treatments helped the plants recover faster from transplant shock. Although the size of the root system was not measured during the course of this experiment, the recovery from the transplant shock may have been caused by a stimulation of new root formation and/or root elongation by these NAA treatments. Dose-dependent increases in both root and shoot dry mass have been reported previously as the result of NAA applications to the roots of vinca (van Iersel, 1998).

Dark respiration was similar in all treatments from 8 to 11 DAT (Fig. 1). During the last 17 d of the experiment, the differences in R_{dark} among the four treatments were very different from those observed from 5 to 7 DAT. From 12 DAT until the end of the experiment, the highest R_{dark} was seen in the 0.025 mg·L⁻¹ treatment, followed by 0.25 mg·L⁻¹. The lowest R_{dark} occurred in the

Fig. 2. The effect of drenches with different concentrations of NAA on the carbon use efficiency (mole C stored in plant dry matter per mole C fixed in gross photosynthesis) of vinca at different times after transplanting seedlings in diatomaceous earth. At one day after transplanting, auxin solutions were applied to the root zone of the plants (36 mL/plant). Solid lines indicate a significant quadratic correlation ($P < 0.05$) between the NAA concentration and carbon use efficiency. The NAA concentration was transformed by $\log(\text{conc} + 0.0025)$ before regression. Note the different Y-axis scale on day 6.



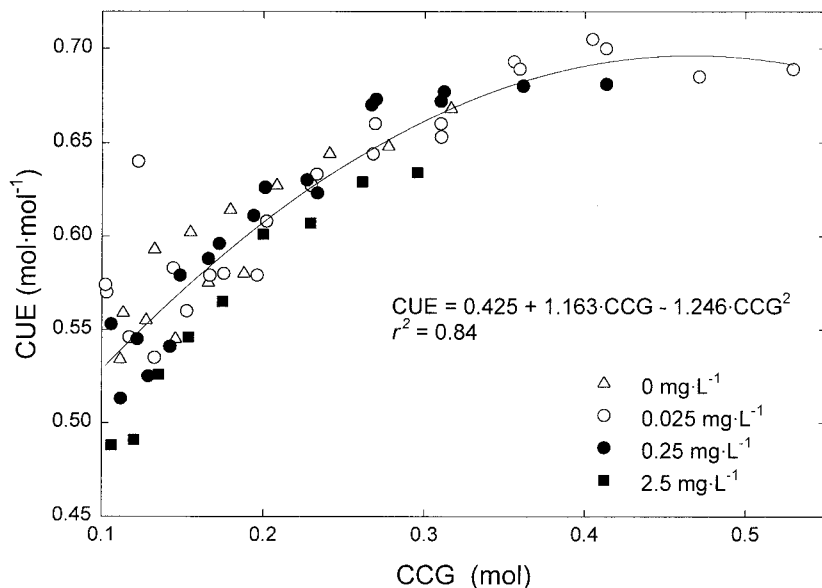


Fig. 3. The relation between carbon use efficiency (CUE, mol C stored in plant dry matter per mole C fixed in gross photosynthesis) and cumulative carbon gain (CCG, mol C fixed by the plants since the start of the experiment) of vinca as affected by NAA applications. At 1 d after transplanting, auxin solutions were applied to the root zone of the plants (36 mL/plant). Only data with a CCG of >0.1 mol is included, because of large changes in CUE of very small seedlings. The solid line is a second-order polynomial, fitted through all the data in the graph.

2.5 mg·L⁻¹ treatment during this period. At this stage, differences in R_{dark} were probably no longer due to the effects of transplant shock, but caused by differences in plant size and growth rate. The plants in the 0.025 and 0.25 mg·L⁻¹ treatments were larger and grew faster than those in the other two treatments. Thus, both maintenance and growth respiration would be expected to be higher in the 0.025 and 0.25 mg·L⁻¹ treatments, which explains the observed differences in R_{dark} .

Differences in growth do not only depend on photosynthesis, but also on the efficiency of the conversion of carbohydrates into dry matter. There were significant differences in CUE among treatments from 11 DAT until the end of the experiment (Fig. 2). The highest CUE was seen in the 0.025 mg·L⁻¹ treatment, while the CUE in the 0.25 mg·L⁻¹ treatment was similar to that of the control treatment. Carbon use efficiency consistently was lowest in the 2.5 mg·L⁻¹ treatment. Although these results suggest that NAA had a direct effect on CUE, this may not have been the case. Plotting the CUE against CCG showed that CUE increased with increasing CCG (Fig. 3). Cumulative carbon gain is a direct measure of the growth of the plants since the start of the experiment, and thus of plant size. The strong correlation between CCG and CUE ($r^2 = 0.84$, $P < 0.0001$) suggests that CUE was not directly affected by NAA, but rather that the differences in CUE among treatments were due to differences in plant size. Only data with a CCG of more than 0.1 mol are included in Fig. 3, because the CUE of small seedlings showed large fluctuations shortly after transplanting (Fig. 2). These fluctuations were the result of rapid changes in R_{dark} of the plants (Fig. 1) during the first week after transplanting. A CCG of 0.1 mol is approximately equivalent to a doubling of the size of the transplanted seedlings.

Amthor (1989) has argued that CUE should decline during the vegetative growth phase of crops. This was based on the assumption that a smaller fraction of the total respiration is directly related to plant growth, while an increasing fraction is associated with maintenance respiration. However, there is no convincing evi-

dence that this assumption is necessarily true. Previous results actually indicate that growth respiration of a vinca crop increases more rapidly than maintenance respiration during development (van Iersel, 1999). If crop photosynthesis increases more rapidly than maintenance respiration during plant development, CUE would be expected to increase because a larger fraction of the total available carbohydrates would be used for growth and growth respiration.

Carbon use efficiency of most plants normally ranges from 0.5 to 0.7 (Amthor, 1989; Bednarz and van Iersel, 1998; Gifford, 1995; McCree et al, 1990; van Iersel and Bugbee, 1996), although it strongly depends on growing conditions, such as temperature, light intensity, and day length (van Iersel and Lindstrom, 1999). Carbon use efficiency of the vinca seedlings was relatively low during the early part of the experiment (Fig. 3), but reached more typical values (up to 0.7) as the plants became larger. Generally, young plants use 25% to 35% of their daily assimilates to support growth and 1.5% to 3% for maintenance processes (Hay and Walker, 1989), which would result in a CUE of 62% to 74%.

The strong correlation ($r^2 = 0.98$) between the total carbon gain of the plants during the experiment and the dry mass of the plants (Fig. 4) indicates that the CER measurements gave an accurate indication of plant growth.

The differences in CER and CUE among the treatments also were reflected in the final dry mass and leaf area of the plants (Table 1). Leaf area, shoot dry mass, and root dry mass in the plants treated with NAA at 0.025 mg·L⁻¹ were increased by 73%, 50%, and 36% as compared to control plants, respectively. This increase in growth as the result of auxin applications was smaller than that reported earlier with greenhouse-grown plants (260%; van Iersel, 1998), but still substantial. This difference in response may have been caused by differences in the age of the plant material. The seedlings in this study were ≈ 10 d older than those used by van Iersel (1998) and the effect of auxin treatments on root growth depends on the initial elongation rate of the roots (Pilet and

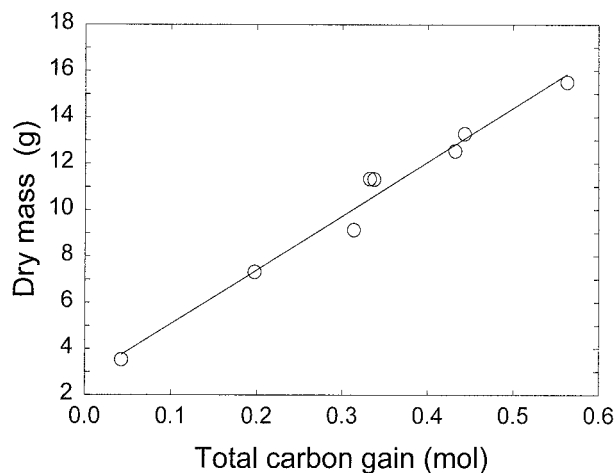


Fig. 4. Total measured carbon gain (TCG) of the plants during the experiment versus their final dry mass. The close correlation between these parameters (dry mass = 2.77 + 23.23 × TCG, $r^2 = 0.98$) confirms that the CO₂ exchange measurements are an accurate measurement of plant growth.

Table 1. The effect of different rates of NAA on posttransplant growth of vinca seedlings. Seedlings were treated with 36 mL of NAA solution per plant at 1 d after transplanting. Dry weight and leaf area were determined at 28 d after transplanting.

NAA concn (mg·L ⁻¹)	Leaf area (cm ²)	Dry wt (mg)			Shoot-root ratio
		Shoot	Root	Plant	
0	41.4	226	107	333	2.12
0.025	71.8	339	146	486	2.34
0.25	70.4	304	150	454	2.03
2.5	23.2	150	76	226	1.97
Significance					
Quadratic	**	*	*	*	NS

NS, **, *** Nonsignificant or significant quadratic correlation at $P < 0.05$ or 0.01 , respectively. The NAA concentration was transformed by $\log(\text{conc} + 0.0025)$ before regression.

Saugy, 1986), and thus on the developmental stage of the plants.

Although the rationale behind the experiment was to minimize transplant shock by increasing root growth, there were no differences in shoot-root ratio at the end of the experiment (Table 1). This corroborates the findings of van Iersel (1998), who found that auxins can stimulate posttransplant growth without a significant effect on shoot-root ratio. Therefore, it is not clear whether the increased growth as the result of 0.025 and 0.25 mg·L⁻¹ NAA is the result of increased root growth. However, it is possible that increases in root growth are almost immediately matched by increases in shoot growth, especially if the shoot growth is limited by the ability of the roots to absorb water and/or nutrients. This might be the case after transplanting bare-root seedlings, because significant root damage is likely to occur during handling of the tender roots.

Conclusion

Posttransplant growth of bare-root vinca seedlings was significantly increased by NAA applications of 0.025 and 0.25 mg·L⁻¹, but auxin applications did not affect the shoot-root ratio of the plants. It is not clear whether the observed growth responses are the result of increased root growth or of another physiological process. Drenches with NAA had significant effects on both whole-plant P_{net} and R_{dark} . This effect was dose-dependent. From 6 to 8 DAT, NAA applications of 0.025 and 0.25 mg·L⁻¹ decreased R_{dark} , suggesting that these plants recovered from transplant shock more quickly than control plants. The 0.025 and 0.25 mg·L⁻¹ treatments resulted in increased P_{net} , R_{dark} , and CUE during the latter part of the experiment, indicating a higher growth rate. These changes in CER were reflected in the final shoot and root dry mass and leaf area of the plants. The highest concentration of NAA tested (2.5 mg·L⁻¹) proved to be slightly phytotoxic and reduced the growth of the seedlings. These results show that NAA can be used to improve posttransplant growth of bare-root vinca seedlings, but the effects of NAA are strongly dependent on the applied amount.

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