Nitrogen Form and Concentration Affect Nitrogen Leaching and Seedling Growth of *Prosopis velutina*

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Abstract. Velvet mesquite (*Prosopis velutina* Woot., Syn.: *P. juliflora* (Swartz) DC. var. *velutina* (Woot.) Sarg.) has become more popular in arid landscapes of the southwestern U.S., but little information on N requirements during the seedling stage is available. In addition to optimize growth of seedlings, minimizing N in runoff during production is an important consideration. Experiments were conducted to determine how biomass production and N leaching were affected first by different ratios of ammonium and nitrate N in sand culture and second by different N concentrations when seedlings were grown in two substrates. Mesquite seedlings produced the greatest biomass after 120 days when fertigated with a solution of 33 NO$_3^-$ : 67 NH$_4^+$ . Loss of N through leachate was 40% greater when NH$_4^+$ compared to NO$_3^-$ was used or more compared to one third or none in the fertigated solution. Nitrogen in leachate was highest after 16 weeks of treatment, coinciding with the reduced growth rate of seedlings. The second experiment utilized either sand or commercial growing media and a fertigation solution of 33 NO$_3^-$ : 67 NH$_4^+$ . Fertilization with 200 mg·L$^{-1}$ N after 60 days in either substrate produced greatest biomass, while rates of 25, 50, or 100 mg·L$^{-1}$ N produced about half of that biomass. With few exceptions, less N in either form was found in leachate when seedlings were grown in media and were fertigated with the two higher N rates compared to seedlings grown in sand at the two higher N rates. Plant morphology, biomass accumulation, photosynthetic allocation, and the fate of N in the growing substrate and in leachate were strongly affected by the choice of growing substrate.

Arizona or velvet mesquite (*Prosopis velutina* Woot., Syn.: *P. juliflora* (Swartz) DC. var. *velutina* (Woot.) Sarg.) is a semi-deciduous tree native to the Sonoran desert and is a common plant in wild, naturalized, and planned landscapes in xeriscapes of the southwestern U.S. (Jones and Sacamano, 2000). Demand for this native species has increased recently because it tolerates a wide range of arid soil types and is an asset in low water landscapes as well as in lawn areas. Nutrient requirements of common southwestern woody plants during container production are not well studied. *P. velutina* is a member of the legume family and under natural conditions forms a biological symbiosis with nitrogen-fixing organisms. Soils under the crowns of legumes in the desert usually have 10 times more N (0.3%) than those under non-nitrogen fixers (0.03%) (Felker and Bandurski, 1979). However, fertilizer is routinely added to legumes in container nursery production for plants to reach marketability in a timely manner.

The form of N that is supplied to plants affects the uptake of other cations and anions, cellular pH regulation, and the soil in the rhizosphere (Marschner, 1995). Nitrogen uptake as nitrate or ammonium accounts for about 80% of the total cation or anion import. Ammonium uptake generally causes a decrease in pH of the rhizosphere. Barker and Mills (1980) state that although most cultivated plants preferentially take up nitrate over ammonium, alkaline soil conditions or nutrient solutions buffered at neutral often resulted in favorable growth response of plants supplied predominantly with the ammonium form of N.

Several species of ornamental plants have produced greater dry weight when supplied with 50% or more ammonium compared to nitrate alone (Aiello and Graves, 1997; Hummel et al., 1990; Ingram and Joiner, 1982). Those results led to the conclusion that plants better adapted to acidic soil conditions seem to prefer ammonium, while those adapted to alkaline soils prefer nitrate (Aiello and Graves, 1997; Hummel et al., 1990; Ingram and Joiner, 1982). Higher N uptake rates were measured when greenhouse "Royally" roses were supplied with ammonium or ammonium nitrate compared to nitrate alone, but N form had no effect on flower yield or quality (Cabrera et al., 1996).

Fertigation regimes apply nutrients either in a single application or split applications of equal amounts at predetermined time intervals, with the goal of meeting nutritional needs corresponding to growth (Imo and Timmer, 1992). Typically, soluble N is applied in irrigation water at concentrations of 100 to 200 mg·L$^{-1}$ once or twice weekly (Mills and Jones, 1996). Fertilization often exceeds actual N requirements and smaller, more frequent doses accompanied with tissue analysis are recommended to determine concentrations needed for optimum growth (Mills and Jones, 1996). Imo and Timmer (1992) used different fertilization schedules with the goal to maintain a steady-state of tissue nutrient concentration in mesquite (*Prosopis chinensis* Mol.) seedlings and found differences in N uptake efficiency, but no difference in biomass production.

The objectives of the experiments were to determine how velvet mesquite biomass production and N leaching were affected first by fertigation with different ratios of ammonium and nitrate in sand culture and second by different N concentrations in the preferred ratio when seedlings were grown in two substrates.

Materials and Methods

Nitrogen form, *Prosopis velutina* seeds were germinated in Cone-tainers (Stuewe & Sons, Inc. Corvallis, Ore.) (164 mL volume) with 20-grade pure silica sand in June 2002 under mist in a greenhouse at the University of Arizona in Tucson, Ariz. Uniform seedlings with two true leaf pairs were selected and assigned to treatments. Hoagland’s solution (Hoagland and Arnon, 1950) was prepared and N was added as (NH$_4$)$_2$SO$_4$ and/or KNO$_3$ to formulate four treatments of the following ratios of NO$_3^-$ : NH$_4^+$. 100:0, 67:33, 33:67, and 0:100. Plants were fertigated with 100 mg·L$^{-1}$ N in the different ratios twice a week. On fertigation days each seedling received 30 mL solution four times throughout the day. Irrigation with tap water was applied in the same amounts the other days. After 12 weeks, both irrigation and fertigation events were reduced to two times per day for the remaining 4 weeks.

Average minimum and maximum temperatures in the greenhouse were 19 and 33°C, respectively. Photosynthetically active radiation at canopy level ranged from 600 to 800 µmol·m$^{-2}$·s$^{-1}$.

Two randomly chosen seedlings per block and treatment were harvested destructively 40, 80, and 120 d after fertigation treatments began. Seedlings were dried for 96 h at 65°C and shoot and root dry weights were recorded. Shoots of seedlings harvested 120 d after onset of treatments were analyzed for total N by the Kjeldahl method (Jones, 1991). Leachate was collected every 4 weeks beginning with a fertigation day until just before the next scheduled fertigation. Nitrate and ammonium in leachate were measured with ion-selective electrodes (Thermo Orion, Beverly, Mass.).

The experiment was arranged in a completely randomized block design with three blocks per treatment. Nine seedlings were...
Nitrogen concentration. *Prosopis velutina* seeds were sown in June 2003 in Cone-tainers filled with 20:80:1:1 peat:vermiculite:perlite (Sunshine Mix 1, Sun Gro Horticulture Distribution, Inc., Bellevue, Wash.). Physical characteristics of the media were determined according to Davidson et al., (2000). EC and pH were determined with a 1:1 (by volume) saturated paste extract. Both substrates were leached with tap water before seeds were sown at the beginning of the experiment.

Nitrogen at a ratio of 67 NH₄⁺ : 33 NO₃⁻ was provided in a Hoagland's solution (Hoagland and Arnon, 1950) at concentrations of 25, 50, 100, or 200 mg L⁻¹. Each seedling received 40 ml of nutrient solution three times daily twice a week. Starting 2 weeks after seedling emergence, all seedlings received 25 mg N/L for the first three fertigations days followed by the assigned concentrations for the remainder of the experiment. The day when fertigation treatments started was considered the first day when plants received the assigned treatments. Irrigation with tap water was applied four times daily for sand-grown plants and three times daily for media-grown plants at 30 mL each event except on fertigation days.

Minimum and maximum air temperatures in the greenhouse were 20 and 32 °C, respectively, while substrate temperatures of media and sand ranged from 22 to 30 °C and from 24 to 35 °C, respectively. Photosynthetic active radiation at canopy height in the greenhouse ranged from 450 to 740 μmol m⁻² s⁻¹ at midday during the study.

Leachate was collected 15, 36, and 54 d after treatments started on days when fertigation was applied. Samples were collected from three plants per block and treatment. Nitrate N and ammonium N were measured at 25 °C three plants per block and treatment. Nitrate fertilization was applied. Samples were collected from after treatments started on days when fertigation began. The numbers of leaves were counted and seedling shoots and roots were separated. Dry weights were recorded after seedlings were dried at 65 °C. The experiment was arranged in a completely randomized block design with four blocks. Twenty seedlings were grown per block and treatment. Data were analyzed using analysis of variance and when time and N ratios were significant stepwise regression was used to characterize the effects on the different variables. (SAS Institute, Cary, N.C.).

Results and Discussion

**Nitrogen form.** Fertigation of seedlings with different ratios of NO₃⁻ : NH₄⁺ affected shoot and root dry weight and root to shoot ratio at one or more sampling times during the experiment (Table 1). Shoot and root dry weights showed greatest gain from day 40 to day 80, but increased less during the last 40 d of the experiment except for root dry weight of seedlings supplied with 33 NO₃⁻ : 67 NH₄⁺. At the end of the experiment, seedlings receiving 33 NO₃⁻ : 67 NH₄⁺ had greater total biomass than seedlings receiving N only as ammonium or nitrate. The reduced biomass accumulation during the last 40 d of the experiment was probably due to root restriction in the limited container size (Davison et al., 2000). A similar decline in relative growth rate was reported for *Prosopis chilensis* seedlings after 6 weeks, regardless of nutrient concentrations applied (Imo and Timmel, 1992). The root to shoot ratio after 40 and 80 d decreased when the proportion of ammonium in the fertigation solution increased, but at the end of the experiment no differences in root to shoot ratio among treatments were observed (Table 1).

Nutrient solutions containing both ammonium and nitrate resulted in greatest shoot or root dry weight at the end of the experiment, a fact documented for many other species (Barker and Mills, 1980; Marschner, 1995). Woody ornamental species that thrived with a combination of ammonium and nitrate were mountain laurel (*Kalmia latifolia* L.) (Hummel et al., 1990) and Shumard oak (*Quercus shumardii* Buckl.) (Ingram and Joiner, 1982), which seems to require a minimum of 50% NH₄⁺ for maximum growth and prevention of chlorosis. Privet (*Ligustrum ibelium* L.) growth was the same regardless of whether N was applied as nitrate, ammonium or an equal mix of both N forms (Stratton et al., 2001). Higher dry weight in Amur maackia (*Maackia amurensis* Rupr. & Maxim.) (Aiello and Graves, 1997) resulted from solutions with more than half the N supplied by NH₄⁺ compared to NO₃⁻ alone. Trelease and Trelease’s (1935) sand culture solution formulated with 70NH₄⁺ : 30NO₃⁻ enabled a variety of plants, including legumes <40 d old to absorb ammonium more readily than nitrate, which concurs with results for mesquite seedlings in this study. Uptake of ammonium decreased the pH of the rhizosphere because protons are released, whereas nitrate uptake increased external pH due to the release of hydroxyl ions (Trelease and Trelease, 1935). The lower pH in the rhizosphere facilitated uptake of micronutrients.

Shoot N concentrations at the end of the experiment decreased linearly (*p* = 0.007) with decreasing NH₄⁺ in the fertigation solution. Fertigation with 0 NO₃⁻ : 100 NH₄⁺ resulted in 3.0 mg kg⁻¹ N in shoots, followed by 2.0, 2.3, and 1.8 mg kg⁻¹ for plants treated with NO₃⁻ to NH₄⁺ ratios of 67:33, 33:67, and 100-0, respectively. Similarly, higher leaf N contents were found when Shumard oak (Ingram and Joiner, 1982), privet (Stratton et al., 2001) or Amur maackia (Aiello and Graves, 1997) were fertigated with nutrient solutions containing 50% to 100% of ammonium versus nitrate alone. Optimum N tissue content for mesquite species in container cultivation is not published, but mesquite shoot tissue from all treatments was within the general limits for optimum growth, which range from 2 to 5 mg kg⁻¹ of the plant dry weight (Marschner, 1995). Nitrogen in leachate was affected by ratio of N form and time of sampling (Table 2), but not by interactions of the two factors. When ammonium constituted two-thirds or more of the N applied, cumulative N losses for the monitored fertigation events almost doubled compared to treatments receiving two-thirds or more of the N as nitrate. Leachates contained similar ratios of ammonium and nitrate as the ratios in the treatment solutions. Overall, lowest N loss occurred during week 12 and was probably associated with maximum growth rates. The excessive amounts of N leached during

### Table 1. Biomass and root to shoot ratio of mesquite seedlings fertigated with different ratios of NO₃⁻ and NH₄⁺. DAF = days after fertigation started.

| NO₃⁻ : NH₄⁺ | Shoot dry wt (g) | Root dry wt (g) | Root to shoot ratio |
|-------------|-----------------|-----------------|---------------------|
| 40 DAF      |                 |                 |                     |
| 100:0       | 0.23            | 0.40            | 1.94                |
| 67:33       | 0.45            | 0.53            | 1.21                |
| 33:67       | 0.40            | 0.35            | 0.89                |
| 0:100       | 0.40            | 0.39            | 1.05                |
| Significance |                 |                 |                     |
| Linear      | *               | NS              | **                  |
| Quadratic   | *               | NS              | *                   |
| 80 DAF      |                 |                 |                     |
| 100:0       | 0.82            | 0.87            | 1.15                |
| 67:33       | 0.97            | 0.98            | 1.07                |
| 33:67       | 1.66            | 0.81            | 0.52                |
| 0:100       | 0.81            | 0.76            | 0.96                |
| Significance |                 |                 |                     |
| Linear      | NS              | NS              | NS                  |
| Quadratic   | **              | NS              | *                   |
| 120 DAF     |                 |                 |                     |
| 100:0       | 0.91            | 0.96            | 1.17                |
| 67:33       | 1.01            | 1.19            | 1.22                |
| 33:67       | 1.68            | 1.76            | 1.11                |
| 0:100       | 0.86            | 0.98            | 1.16                |
| Significance |                 |                 |                     |
| Linear      | *               | NS              | NS                  |
| Quadratic   | **              | NS              | NS                  |

**NS**: Nonsignificant or significant at *p* < 0.05 or 0.01, respectively.
Table 2. Cumulative N in leachate from one fertigation event collected 4, 8, 12, and 16 weeks after fertigation (DAF) treatments began.

| Substrate | N applied (mg·L⁻¹) | Leaf (no.) | Shoot dry wt (g) | Root dry wt (g) | Root to shoot ratio |
|-----------|--------------------|------------|-----------------|----------------|-------------------|
| 0 DAF     |                    |            |                 |                |                   |
| Media     | 210                | 8          | 0.153           | 0.075          | 2.08              |
| Sand      | 210                | 8          | 0.153           | 0.075          | 2.08              |
| Significance | Linear | NS | NS | NS | NS |
|           | Quadratic          | NS         | NS              | NS             | **               |
| 4 DAF     |                    |            |                 |                |                   |
| Media     | 210                | 8          | 0.153           | 0.075          | 2.08              |
| Sand      | 210                | 8          | 0.153           | 0.075          | 2.08              |
| Significance | Linear | NS | NS | NS | NS |
|           | Quadratic          | NS         | NS              | NS             | NS               |
| 8 DAF     |                    |            |                 |                |                   |
| Media     | 210                | 8          | 0.153           | 0.075          | 2.08              |
| Sand      | 210                | 8          | 0.153           | 0.075          | 2.08              |
| Significance | Linear | NS | NS | NS | NS |
|           | Quadratic          | NS         | NS              | NS             | NS               |
| 12 DAF    |                    |            |                 |                |                   |
| Media     | 210                | 8          | 0.153           | 0.075          | 2.08              |
| Sand      | 210                | 8          | 0.153           | 0.075          | 2.08              |
| Significance | Linear | NS | NS | NS | NS |
|           | Quadratic          | NS         | NS              | NS             | NS               |

NS**NS nonsignificant or significant at P < 0.05 or 0.01, respectively.

In the media and to examine uptake of ions by plants without the complicating factor of ion exchange capacity of commonly used media. However, in sand culture much larger quantities of nutrients are discharged through leachate, while in media with greater cation exchange capacity ions could be stored and later absorbed by plants in between fertigation events. Different ratios of N form affected NH₄⁺ and NO₃⁻ losses in leachate with NO₃⁻ accounting for 75% to 98% of the N losses when N was applied as ratios of NO₃⁻ to NH₄⁺ ratios of 70:30 to 40:60 (Gammore-Neuman and Hagiladi, 1992). While this report contrasts with our results, they reported, similar to our study, increased N leaching losses from geranium (Pelargonium zonale ‘Empress’) growing in tuff over a study period of 10 weeks.

Results from this experiment suggest that optimum growth of mesquite seedlings can be attained by providing up to two thirds of the N in the less expensive ammonium form. Nitrogen supply should be reduced in fall when seedling growth declines in response to environmental cues. Timely transplanting will prevent retarded growth during the growing season and minimize loss of N through leachate.

Nitrogen concentration. Physical characteristics of the commercial medium (Table 3) were within the recommended range for container media (Davidson et al., 2000). Porosity and air space of sand were within the recommended range for container media, while bulk density was too high, and water-holding capacity was too low (Table 3). Although plants were watered frequently, it is possible that the low water holding capacity may have contributed to some stress of plants, resulting in less biomass production and a higher root to shoot ratio, especially in the beginning of the experiment. High bulk density has been shown to restrict root extension and shoot growth (Masle and Passioura, 1987). EC and pH of the substrates were different at the beginning of the study, but leaching with tap water reduced EC in the commercial medium to <0.5 dS·m⁻¹. Substrate pH equilibrated to 7.3 for sand and pH of commercial media ranged from 8.0 to 6.9 with increasing N concentration.

Leaf number was greater for media-grown seedlings than for those grown in sand at 20 and 60 d after fertigation (Table 4). Nitrogen concentration increased leaf number of plants grown at the highest N concentration at 60 d after fertigation, but had no effect on leaf number during the first two sampling periods (Table 4). The most noticeable difference in leaves observed during production was the relative size. Media-grown seedlings produced larger, softer leaves compared to those produced in sand. Both substrates and fertilizer concentration affected plant morphology. Plants in either substrate receiving 200 mg·L⁻¹ N were taller (data not shown) and more succulent compared to seedlings fertigated with lower N concentrations. Sand-grown plants appeared more woody compared to softer media-grown seedlings. Water stress limited growth of two woody ornamentals to a greater extent than lower concentrations of fertilizer (Rose et al., 1999). They also reported that plants under water stress were more compact than well-watered plants, similar to sand grown plants in our study.

Sand-grown seedlings had greater root dry weight and root to shoot ratio than those from substrate at the end of treatments (Table 4). At 20 d after fertigation, shoot dry weight of plants in media was almost three times greater compared to seedlings grown in sand. Nitrogen concentration had no influence on growth at that time. At 40 d after fertigation, shoot dry weight was greater and root to shoot ratio was less for seedlings in media compared to sand. Increasing N concentration also resulted in increasing shoot dry weight at that time (Table 4), while none of the other variables were affected by N concentration.

At 60 d after fertigation, plants in media had accumulated a greater number of leaves and more shoot and total biomass than those growing in sand. Seedlings receiving the 200 mg·L⁻¹ N treatment had the greatest biomass and smallest root to shoot ratio (Table 4). The only interaction between media and N
rates was found for root dry weight at day 60. Root dry weight of sand-grown seedlings increased from 0.50, 0.53, or 0.59 g to 0.96 g from the lowest to the highest N concentration, respectively. However, root dry weight of media-grown seedlings was 0.57 g for both the highest and lowest N concentration and 0.44 g for the other two treatments. Imo and Timmer (1992) found that increasing N application to mesquite seedlings increased shoot growth, but not root growth over the same range of total N applied as in this experiment. Our experiment confirms their conclusion that shoots appear to be more sensitive to increasing fertilizer levels than roots. This lack in sensitivity of mesquite seedlings to respond to a range of increase in N application suggests that once a minimum of N is supplied, plants use that base level for growth, but may take up the additional N to increase their internal N concentration which may be mobilized later for growth if N uptake may become limiting (Imo and Timmer, 1992). Privet showed the same trend of increasing shoot dry weight when N concentrations increased from 0 to 50 mg·L⁻¹ but shoot growth remained the same with fertigation of 50 to 300 mg·L⁻¹ N, while root growth was constant over the entire range of N concentrations (Stratton et al., 2001). Nitrogen concentration in privet shoots increased when plants were supplied with up to 100 mg L⁻¹ N, but in roots N concentrations increased only from 0 to 25 mg·L⁻¹ N and levels of N concentration in the plants remained the same with fertigation solutions up to 300 mg·L⁻¹ N.

The greater root to shoot ratio initially observed for seedlings in sand before fertigation began was maintained throughout the experiment (Table 4). Lower moisture-holding capacity of sand which could cause temporary moisture deficits between irrigations or nutrient deficiency can result in greater carbohydrate allocation to roots than shoots (Nilsen and Orcutt, 1996). Substrate with high soil bulk density has been documented to restrict root extension, decrease shoot growth, and photosynthesis (Masle and Passioura, 1987) and increase the root to shoot ratio (Masle and Farquhar, 1988). Nitrogen concentration did not affect the root to shoot ratio during the first 40 d of fertigation, until 60 d after fertigation when seedlings fertilized at 25 mg·L⁻¹ N increased shoot growth at a slower rate than root growth. The allocation of more carbohydrates to roots than to shoots under nutrient deficient conditions has been observed in P. chilensis (Imo and Timmer, 1992) and other woody plant species (Henry et al., 1992; Lea-Cox and Syvertsen, 1996). It may be an adaptive mechanism of plants to expand the root system to increase the area where absorption of nutrients will occur (Imo and Timmer, 1992).

Some sand-grown plants fertilized with 200 mg·L⁻¹ N developed nodules by 60 d after fertigation, indicating inoculation with nitrogen-fixing bacteria. Inoculation and consequent symbiosis requires about 6 weeks before it becomes visually detectable. Alkaline soil conditions and a sufficient supply of N from the time of infection and onset of N₂ fixation are favorable during this time when growth of the bacteria and the nodule tissue rely on the host organism for supply (Marschner, 1995).

Leachate collected 15 d after fertigation contained similar amounts of N when seedlings in both substrates were fertigated at 25, 50, or 100 mg·L⁻¹ N (Fig. 1). Fertigation at 200 mg·L⁻¹ N resulted in the highest amount of NH₄⁺-N discharge from seedlings in sand.

Fig. 1. Nitrate-N and ammonium-N in leachate collected from seedlings grown in sand or commercial media mix and fertigated with different concentrations of N 15, 36, and 54 d after fertigation treatments started. Means of six replications and standard error bars are shown.

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culture, four times greater than from seedlings in media-grown plants. Greater losses of N when higher concentrations of fertigation solutions were applied to very young plants have been reported before and are attributed to a small root system that has explored only partial volume of the growing substrate and the limited N uptake capacity of this small root system (Rose and Biernacka, 1999). At days 36 and 54, greatest N losses in leachate were found as NH$_4$$^+$-N when fertigation at 100 or 200 mg·L$^{-1}$ N was supplied to seedlings in sand. With few exceptions, less N in either form was found in leachate when seedlings were grown in media and were fertigated with the two higher N rates (Fig. 1). The fact that increasing N application rates up to 100 mg·L$^{-1}$ did not increase N in leachate proportional to the application rate but also did not result in a linear increase in dry weight indicates that plants may take up more N to increase their internal N status (Imo and Timmer, 1992, Lea-Cox and Syvertsen, 1996).

Greater losses of N in sand are expected due to the lower cation exchange capacity of sand compared to the organic growing substrate. Low concentrations for NH$_4$$^+$-N in leachate from media is likely due to adsorption of cations by the organic components of the media, and possible nitrification or volatilization. As media-grown plants accumulated more biomass during the study, they could be expected to take up greater quantities of N than the smaller seedlings cultivated in sand.

With increasing fertigation concentration, the ratio of NH$_4$$^+$-N to NO$_3$$^-$$^-$N is greater in leachate from sand substrate, while similar of each N form were found in leachate from media (Fig. 1). Nitrogen forms in leachate from sand were similar to the ratio of 2 NH$_4$$^+$ : 1 NO$_3$$^-$$^-$ in the applied solution, which suggest that there was no preferential uptake of one N form compared to the other. Lower amounts of NH$_4$$^+$-N compared to NO$_3$$^-$$^-$N in the organic substrate suggest nitrification, absorption to the media, while greater uptake of NH$_4$$^+$-N cannot be completely excluded.

In conclusion, rapid growth resulted over 60 d when *P. velutina* seedlings were grown in commercial media. A total of 408 mg N per seedling was applied through fertigation twice a week with a 200 mg·L$^{-1}$ N solution where N was derived from 66% ammonium and 33% nitrate. Leachate losses of N during the first 15 d could be minimized by reducing the highest fertigation rate at that time, and overall N leaching losses can be minimized by using growing substrate with higher water holding capacity and lower bulk density compared to sand and by using fertigation rates lower than 200 mg·L$^{-1}$ N. Healthy seedlings with about half the dry weight were produced with a total of 51 mg N per seedling over 60 d supplied by fertigation solutions as low as 25 mg·L$^{-1}$ N. This rate decreased N in leachate compared to the 200 mg·L$^{-1}$ N fertigation rate, but is likely to result in even lower growth rates if applied for >60 d. While sand is often used as a substrate to investigate plant growth, the results of this study demonstrate that plant morphology, biomass accumulation, photosynthate allocation, and the fate of N in the growing substrate and in leachate are strongly affected by the choice of growing substrate.

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