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ESTABLISHMENT OF UNDERSTORY WOODY SPECIES OF CALIFORNIA CENTRAL VALLEY RIPARIAN HABITATS: NUTRIENT DYNAMICS AND FLOODING TOLERANCE

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ABSTRACT

Reestablishment of a diverse shrub understory as a component of riparian forests and woodlands is critical for biodiversity, wildlife habitat, and riparian vegetation functions including erosion resistance, and filtration of sediment, nutrients and contaminants. *Rosa californica* (California rose) and *Sambucus mexicana* (Blue elderberry) were selected for study as they are found throughout the California Central Valley in several widespread riparian vegetation types. In addition, blue elderberry is a host species for the threatened Valley elderberry longhorn beetle (*Desmocerus californicus dimorphus*). Field and greenhouse studies were conducted to provide basic understanding of establishment requirements and understanding of the nutrient dynamics of the species and ecosystem.

Containerized plants of similar size but high or low internal pools of nitrogen were used in two nutrient dynamics experiments. In the field experiment, they were transplanted to the Cosumnes River Preserve; half were then supplied with slow-release NPK fertilizer, the others with no supplemental fertilization. Plant survival and growth were quantified through two growing seasons (1-1/2 years). In one greenhouse experiment, both high and low N plants were labelled with the stable N isotope, ^{15}N, before transplanting to larger pots where they received one of three levels of nitrogen. These were sequentially harvested in the 28 days following transplant, and evaluated for growth parameters and dilution of ^{15}N by current uptake (unlabelled N) under the different nitrogen regimes. A greenhouse flooding experiment evaluated flooding tolerance of both species. Survival and growth parameters were followed during the 4- and 8-week flooding periods, and during a post-flooding recovery period.

Blue elderberry was more nitrogen-demanding than California rose as its growth slowed much more with nitrogen or nutrient stress. Growth parameters varied with pre-transplant nitrogen and post-transplant nitrogen in the 28-day greenhouse experiment. However, in the 1-1/2 year field experiment, only the NPK field fertilization had a beneficial effect on most growth parameters. Plant productivity was much greater in California rose than in blue elderberry. Spring growth began earlier in plants that received supplemental field fertilization, and earlier in California rose than in blue elderberry.

Both species relied more on internal N stores at transplant (^{15}N labelled) than on current N uptake (unlabelled N) for growth of new leaves when N availability from the substrate after transplanting was low. Growth of blue elderberry plants was more dependent on remobilized N than it was for California rose in the first week after transplant. The two species were very similar by day 28, however, both depending more on internal N stores when the external N supply was low.

The flooding tolerance of blue elderberry was much poorer than California rose in the greenhouse experiment. Mortality was 50% and 25% after 8 and 4 weeks of flooding, respectively in blue elderberry. High mortality of blue elderberry n the field experiment was apparently due in part to poor tolerance of soil saturation.

Although both species are relatively fast growing, there were substantial differences between them in nutrient physiology, growth and survival that have implications for restoration. Establishment can be improved with fertilization; localized, slow-release fertilizer is effective in providing the nitrogen required by blue elderberry. Pre-transplant fertilization can be critical in sites where N availability is limited, particularly if field fertilization is not used. Planting sites for blue elderberry must have good drainage. California rose is tolerant of a broader range of nutrient and flooding conditions.

KEY WORDS: riparian vegetation, plant growth, nitrogen, flood-plain management, ecology

PROBLEM AND RESEARCH OBJECTIVES

Statement of Problem

The gallery forests and valley oak woodlands of California's Central Valley have declined 90 percent or more since European settlement (Katibah 1984; Warner and Hendrix 1985; CSLC 1994). Riparian vegetation has been removed for agriculture, urban development and flood control projects. Altered water flow patterns, and altered flood and disturbance frequencies also can reduce riparian vegetation longevity and reduce natural regeneration (e.g. Rood and Heinze-Milne 1989; Rood and Mahoney 1990). Flood disturbance appears critical for establishment of many riparian species, in part by providing water and nutrient-rich sediments which contribute to the high primary productivity of riparian communities (Major 1977; Holstein 1984; CSLC 1994).

The understory of riparian forests was the subject of this research because of the high biodiversity therein (Gaines 1980), its importance in erosion resistance (Gray and Leiser 1989) and filtering of sediment and chemical pollution (Schlosser and Karr 1981; Phillips 1989), its limited remaining extent in the Central Valley, and the lack of research on the ecological requirements for the establishment or persistence of understory species. What are establishment requirements for riparian species and how are these correlated with the natural flooding and disturbance regime? (e.g. see Stromberg et al. 1991; Van Auken and Bush 1988).

Objectives

The objectives of these studies were: 1) Define the nutrient adaptation characteristics (relative growth rates, biomass and nitrogen allocation patterns, survival) of the two riparian shrub species and the responsiveness of these parameters to variation in nutrient availability. We expected these species to be highly responsive in growth and allocation to addition of nutrients, which could make them sensitive to long periods without pulses of high nutrient availability, unlike more low-nutrient-adapted species (Chapin 1988). 2) Determine, for these species, whether plant nutrient status at outplanting affected growth, survival, and nitrogen (N) uptake when substrate N availability varied. Timmer and Munson (1991) found nutrient loading of the slow-growing black spruce improved outplanting performance. Fast growing species have small luxury reserves of nitrogen on which to draw when uptake is curtailed, e.g. by disturbance or transplanting, and thus we expected them to be highly dependent for establishment on the availability of N in the substrate (e.g. Millard et al. 1990) and less sensitive to internal N pools. Natural establishment after flood disturbance would normally coincide with high nitrogen availability; in managed riparian zones the lack of such pulses could be artificially replaced. 3) Determine the responses of these key shrub species to the interaction of internal N status and substrate nutrient availability. Because transplanting can have detrimental effects, at least temporarily, on root growth and thus nutrient uptake, the interaction of internal nutrient status and substrate nutrient availability could be crucial to the outcome in terms of plant growth and survival. 4) Determine the survival and growth response of these species to simulated flooding of different durations. Soil saturation may correlate with the distribution of *Sambucus mexicana* on levee slopes and upper terraces (USFWS 1991), where duration and frequency of flooding would be minimal and drainage better. *Rosa californica*, on the other hand, is found in many more commonly flooded microhabitats in the riparian zone.

METHODOLOGY

Research sites & plant materials

1. Field site. The field experiment was conducted at the Cosumnes River Preserve (38°16′N,121°26′W, elevation 1.5 meters) in California's Central Valley. The Preserve covers 5,500 acres near the confluence of the Cosumnes and Mokelumne Rivers, and encompasses riparian forests, oak woodland, and adjacent agricultural land, much of it previously occupied by riparian vegetation. Cooperative efforts of The Nature Conservancy, Ducks Unlimited, Bureau of Land Management, CA Dept. of Fish and Game, and the County of Sacramento are restoring native riparian vegetation by levee removal to encourage natural regeneration and active revegetation of riparian trees, shrubs and grasses. The experimental area, adjacent to Lost Slough, is part of a 96-acre riparian forest restoration project managed by The Nature Conservancy. The site typically floods every year with winter storms. The soils are a mosaic of poorly drained, high-clay soils with a shallow water table and hardpan at variable depths; Dierssen sandy clay loam and Dierssen clay loam predominate (USDA 1991).

2. Greenhouse sites. Complementary greenhouse experiments were conducted on the campus of the University of California at Davis. The ^{15}N study utilized 3:1 fritted clay/sand as the planting media to facilitate manipulation of plant nitrogen availability (Van Andel and Jager 1981). Yolo silty clay loam from the campus fields (UCD 1981) was used for the flooding experiment.

3. Plant materials. Seedlings of the two species *Sambucus mexicana* C. Presl (Blue elderberry), and *Rosa californica* Cham. & Schdl. (California rose)(Hickman 1993) were grown with adequate water and nutrients prior to each experiment. The seeds were collected by The Nature Conservancy at the Cosumnes River Preserve.

Experiments

1. Field experiment. This was a randomized complete block design with a factorial combination of species, seedling nitrogen pool status and soil nutrient availability. The nitrogen internal pool treatment factor had high and low nitrogen levels. The nitrogen-phosphorus-potassium (NPK) post-transplant availability factor was provided by adding a slow release fertilizer to half the planting sites. Outplanting was in the fall, with

March and May harvests for growth analysis, and survival censuses for 1-1/2 years after transplant.

2. Greenhouse ^{15}N transplant experiment. This experiment utilized the same pre-transplant nitrogen treatment as the field experiment and three levels of nitrogen availability after transplant. For five weeks prior to transplant, available nitrogen was ^{15}N-enriched, so the nitrogen source for post-transplant growth could be determined--internal reserves versus from current uptake (Figure 1). Plants were sequentially harvested in the 28 days following transplant.

3. Greenhouse flooding experiment. This was a randomized complete block design with five blocks, the two species, and three flooding treatments (4 weeks, 8 weeks, and no flooding) (Figure 2). Seven weeks before use in this experiment, plants were transplanted to 3-gallon Treepots® (Stuewe & Sons, Corvallis, Oregon), provided with Osmocote slow-release fertilizer for high nutrient availability, and given adequate water. Flooding was initiated under climatic conditions simulating winter dormancy, with spring climatic conditions (increased temperature and light) initiated 2 weeks before the long-flood plants were drained. All plants were harvested 1 March, which allowed 2-1/2 and 6-1/2 weeks recovery after draining for the short- and long-flood plants, respectively. Growth parameter measurements and survival data were collected.

Statistics

Survival data for *Sambucus mexicana* in the field experiment was evaluated with Kruskal Wallis and Mann Whitney non-parametric tests. Analyses of variance were used for most data analyses, with repeated measures for serial harvests from subplots of field data, and for non-destructive canopy volume analyses of field and greenhouse flooding data. The relative growth rate (RGR) differences between treatments were statistically evaluated as treatment* linear time interactions in ANOVAR procedures with ln transformed leaf area, biomass, and canopy volume as dependent variables (Poorter and Lewis 1986; Wandera et al. 1992). Transformations were performed before analysis to address possible violations of equal variance and normality assumptions (Steel and Torrie 1980). The Huynh-Feldt probability adjustments were used where available to address non-independence of repeated measurements of the same plants (Potvin et al. 1990). The 0.05 level of significance was used for all hypothesis tests. Most statistical analyses were conducted with SAS/GLM procedures (SAS Institute 1988).

RESULTS AND SIGNIFICANCE

Field experiment

The pretreatment produced plants of high and low nitrogen pools, and the fertilized subplots had higher soil inorganic nitrogen 2 and 5 months after transplanting, but not after 12 months.

All *R. californica* plants that were not destructively harvested survived through the 1-1/2 years study. Mortality was high in *S. mexicana*--31 alive and 108 dead out of 139 unharvested plants at one year. Two periods of high mortality were noted, the first during the dormant period when winter flooding occurred, and the second associated with July flood irrigation. One month after the July 1993 irrigation, 80% of *S. mexicana* plants appeared stressed, particularly in area I (blocks 1-4). They were either dead or most foliage was brown and new shoots or branches were emerging. Mean redox potential on 6 March was 473.6 mV for area I (blocks 1-4) compared to mean redox potential for area II (blocks 5-8) of 292.4 mV ($p<0.000022$, T-test) . Area I thus was in the oxidized redox potential range of aerated soil, and area II in the moderately reduced range of waterlogged soil (Patrick 1981). Prolonged soil saturation and associated moderately reducing conditions were probably the cause of high dormant-season mortality in *Sambucus mexicana*. This is supported by the greenhouse flooding experiment (see below).

Plants which received field fertilization (high postNPK) had greater projected canopy volumes (ln cm3) during spring growth (19 March - 28 May) than plants without field fertilization (low postNPK). In *Rosa californica*, the growth rate was higher in high postNPK vs. low postNPK plants; high postNPK plants had higher growth rates if they received low preN treatment before transplant, but low postNPK plants had higher growth rates if they were treated with high preN (Table 1, Figure 3). Canopy volume-RGR response to treatments were represented by significant linear time*postNPK and time*preN*postNPK in *Rosa californica*. In *Sambucus mexicana*, no nutrient responses were detected, but the ranking of canopy volume was the same as in *R. californica* (Figure 3: low/high > high/high > high/low > low/low). Relative growth rates in *Sambucus mexicana* were reduced to a greater extent by nutrient stress than the RGRs of *Rosa californica* (Table 2).

Leafout (i.e. new leaf growth after winter dormancy) was earlier in *R. californica* than in *S. mexicana*, and was earlier in plants of both species which received field fertilization. Competition and water stress were minimized in this experiment, but under natural field conditions, early growth could provide a major advantage over later-emerging annual competitors, as the plants could take up water and nutrients and establish a canopy before competition with annuals became intense. Potential disadvantages could be increased susceptibility to late frosts or late flooding--greater sensitivity to growing season flooding relative to dormant season flooding has long been recognized (e.g. Gill 1970).

The nitrogen pool (N mmol/plant) was greater in high than low postNPK plants in both species, averaged over time; *S. mexicana* high postNPK plants gained significantly more nitrogen through time than low postNPK plants (Figure 4). The N concentration of newly expanded leaves one year after planting did not vary with nutrient treatment, however, *S. mexicana* leaves had 3.28 %N compared to 2.33 %N in *R. californica* leaves.

The nitrogen efficiency ratio (NER: $DW_{\text{plant part}}/N_{\text{plant part}}$) is the reciprocal of the nitrogen concentration and indicates the efficiency with which biomass is produced with the amount of nitrogen acquired by the plants (O'Sullivan et al. 1974, Gerloff and Gabelman 1983; for calculations see Chirman 1994). Low postNPK plants had much more biomass per unit of N (or lower N%) at the first harvest than high postNPK plants for whole plant, leaf and root, but were similar in all measures and for both species at the second harvest (Figure 5). *R. californica* had markedly higher NERs than *S. mexicana* and altered its pattern more dramatically than *S. mexicana* in the harvest interval (Figure 5). The high initial NER values indicate that the plants with lower nutrient availability were invested largely in low-N tissues, such as roots, at the time of the first harvest and increased investment in higher-N tissues to approximate the other treatments by the second harvest. A high nutrient use efficiency is advantageous, as it enables a plant to produce substantial biomass at a given nutrient supply rate, thus producing more leaves and roots for acquisition of carbon and nutrients (Chapin 1987). High NER also contributes to an ability to compete for light in dense early successional riparian vegetation. On a whole plant basis, a high NER reflects the larger proportion of biomass allocated to tissues with low N concentration, such as roots and woody stems (Chapin 1987).

Greenhouse ^{15}N Transplant Experiment

All plants in this experiment increased in canopy volume from day 0 to day 28. *Rosa californica* grew faster than *Sambucus mexicana*, high postN and mod postN plants grew faster than low postN (high > mod > low), and high preN plants generally grew faster than low preN plants (Table 3; Figure 6). Rapid growth in *S. mexicana* high postN plants began about 10 days after transplant in both the high and low preN plants, but was slightly earlier in high preN plants. By 28 days, high postN plants of both species had greater canopy development than mod postN plants, which had greater canopy development than low postN plants. Treatment differences in canopy volume-RGRs were represented by significant linear time*treatment interactions--

species, pretreatment N, post-transplant N, and species*post-transplant N (Table 3). In this short-term experiment, estimated canopy volume relative growth rates of *Sambucus mexicana* high postN plants (high and low preN) were about double those of *Rosa californica*. This suggests greater potential growth rates in *S. mexicana*, consistent with its high N requirement.

Twenty-eight days after transplanting, *R. californica* plant biomass was greater than that of *S. mexicana*, and the ranking of plants by their preN/postN treatment combination was the same in both species (see Table 4).

The pretreatment produced similarly-sized plants of high and low internal pools of nitrogen (Figures 6,7). High preN plants of both species had larger N pools at transplant than low preN plants (high preN R 1.34, S 1.62; low preN R 1.06, S 1.54 mmol). During the 28 days following transplant, high preN plants maintained higher N pools than low preN plants (Figure 7). At the final harvest (28 d), the species' N pool was about the same (R 3.27 mmol vs. S 3.06 mmol), and the ranking of N pool size was the same for the two species: high/high > low/high > high/mod > low/mod > high/low > low/low. The N accumulation rates in the high postN plants were more than twice that in mod postN for both species, and almost 7 times that of low postN.

The nitrogen specific absorption rate (N-SAR) is the mmol N absorbed per gram root weight per day (McArthur and Knowles 1993; for calculations see Chirman 1994). All treatment groups with low preN had lower N-SAR values than the high preN plants in the first harvest interval (0-3.5 days). *S. mexicana* plants absorbed less N per unit of root mass than *R. californica* plants at every level of external N supply, when the N-SAR was averaged over the 28 days (Figure 8). The greatest differences in N uptake rate occurred at 1.6 mM N supply: *R. californica* rates were much higher than *S. mexicana* rates, and high preN rates were much higher than low preN rates. At postN 4 mM N supply, *R. californica* N uptake rates remained much higher than *S. mexicana* rates.

The recovery of ^{15}N in unexpanded leaves indicates the relative contribution of internal N stores (at transplant, ^{15}N-labelled) compared to newly acquired N (^{14}N with only natural abundance of ^{15}N)(see Chirman 1994 for calculations). The proportional contribution of internal N to leaves expanding after transplant was markedly higher in *S. mexicana* than in *R. californica* (Figure 9). This is consistent with the greater N-SAR in *R. californica*, which had more rapid current nitrogen uptake as indicated by greater dilution of the pre-transplant ^{15}N. Nitrogen from current uptake contributed strongly to leaf growth by 14 days after transplant, where the external N supply was moderate or high, in both species (Figure 9). After only 28 days, the proportion of remobilized N appeared to depend solely on the external N supply, and was very similar between species. The atom % ^{15}N excess of unexpanded leaves were higher than in other plant parts or the plant average; values initially were greater than one, and much greater than one in *S. mexicana*. This is evidence that the N available for remobilization is from recently incorporated, labeled N pools, and again indicates that *S. mexicana* relies more on remobilized N in the immediate post-transplant period than does *R. californica*. Relative recovery of labelled N remained much higher over time in plants with low N availability after transplant (low postN), indicating remobilization of internal N for new leaf growth (unexpanded leaves). Less dilution of ^{15}N in mature leaves, stems and roots indicated more internal cycling of N (Figure 10). The greatest use of remobilized N was found in the unexpanded leaves of low preN/low postN *S. mexicana* plants in the first two weeks after transplant; uptake capacity of N remained very low in these plants.

Greenhouse flooding experiment

Sambucus mexicana showed poor flooding tolerance relative to *Rosa californica*. *S. mexicana* plants subjected to 8 weeks of flooding had 50% mortality compared to 25% mortality in plants flooded for 4 weeks, and no mortality in control (no-flood) plants (Table 5). Only one *R. californica* plant died, in the 8 week flooding treatment (12.5% mortality); six *S. mexicana* plants died in the whole experiment.

Canopy volume at the completion of flooding of the long-flood plants (8 weeks) varied with the flooding treatment (p = 0.0001), the species (p = 0.0054), and their interaction (p = 0.0001). This analysis used plant measurements taken two weeks after the greenhouse conditions were changed to stimulate growth (supplemental lighting and increased temperature). *S. mexicana* 8-week-flood plants declined in canopy volume during the flooding period by loss of leaves, whereas *R. californica* of the same treatment remained about the same size (Figure 11). Growth inhibition by 8-week duration flooding was thus greater in *S. mexicana* than in *R. californica*.

Sambucus mexicana is an obligate host plant for the threatened Valley elderberry longhorn beetle (*Desmocerus californicus dimorphus*; USFWS 1991). Its usual distribution is on levees and terraces, that are less often flooded and have better soil drainage. Its distribution makes it vulnerable to human disturbance during levee maintenance and agricultural use of higher floodplain terraces (USFWS 1987, 1991). When development projects remove *Sambucus* plants, the Endangered Species Act requires mitigation--transplanting the shrubs or planting replacements. Knowledge of its flooding tolerance is critical in planting site selection for this species, given its sensitivity to soil saturation and high mortality in both the field and flooding experiments.

PRINCIPLE FINDINGS, CONCLUSIONS, AND RECOMMENDATIONS

The results of these experiments are relevant to restoration efforts, which often utilize container-grown plants that are transplanted into natural areas. These species, *Rosa californica* and *Sambucus mexicana* can also be planted for specific goals such as agricultural buffers to reduce runoff of nutrients and sediments to improve water quality of adjacent streams, or for erosion control of streambanks (e.g. Peterjohn and Correll 1984; Phillips 1989).

Evaluation of plant growth responses to fertilization also provides understanding of the response of riparian species to nutrient flushes that naturally occur in riparian habitats with litterfall of deciduous vegetation and deposition of nutrients by overbank flooding. The natural hydrologic regime of California Central Valley rivers included annual flooding with winter rains in the watershed or snowmelt in the spring. Flood control and water diversion have reduced overbank flooding, which provided not only supplemental water but also deposition of nutrient-rich sediments. Two of these experiments investigated the nutrient components of establishment, which can also be used to develop criteria for artificial replacement of flood-deposited nutrients by fertilization in managed riparian systems.

A primary finding of these studies is the differential responses of *Rosa californica* and *Sambucus mexicana* to nutrient additions and nutrient stress. *S. mexicana* is a much more nitrogen-demanding plant, requiring more N for the same amount of growth, and having its growth rate reduced to a much greater extent under nutrient-limiting conditions. *S. mexicana* acquired less nitrogen than did *R. californica*, and in addition used it less efficiently in producing leaf area during the critical period early in the growing season.

Leafout was earlier in plants of both species exposed to high nutrient availability from the substrate. At least in the field conditions of persistent soil saturation encountered in this study, leafout was also much earlier in *R. californica* than in *S. mexicana*. Early leafout, and the high investment of *R. californica* in leaf area per unit of N early in the growing season, could be a critical ecological advantage, as plants could establish canopy early and shade potential competitors (van Andel and Jager 1981; van Andel and Biere 1990).

Higher mortality in *S. mexicana* than in *R. californica* was found in plants exposed to soil inundation and low redox potentials in a greenhouse flooding experiment. Poor tolerance of saturated soil conditions was the most probable explanation for high mortality in *S. mexicana* in the field study as well. Soil saturation may also correlate with the distribution of *S. mexicana* on levee slopes and upper terraces (USFWS 1991), where duration and frequency of flooding would be minimal and drainage better.

These studies provide information on the ecological requirements of establishment for California rose and blue elderberry. This information can be utilized to improve establishment procedures for the species in revegetation efforts and site selection for improved survival of revegetation plantings. Better understanding of the species' requirements can also improve management of mature stands to enhance natural regeneration.

Several recommendations for revegetation or restoration projects using riparian shrubs are suggested based on our experimental results:

1) Field fertilization is recommended for rapid establishment; *R. californica* and especially *Sambucus mexicana* growth was stimulated by NPK fertilization. Localized fertilization, whereby slow-release fertilizer is added to the root zone of the target species, would minimize the growth stimulation to competing plant neighbors.

2) A pretreatment pulse of high nutrients might be beneficial, especially if the planting site is of low fertility and field fertilization is impractical or proscribed by the revegetation permit/contract. However, a short period of nutrient deprivation just prior to trans-planting to a high-fertility site may stimulate root growth and uptake of nutrients. This could be an adjunct to field fertilization.

3) Appropriate site selection seems to be very important for *Sambucus mexicana*, which requires high nutrients and is also relatively intolerant of prolonged soil saturation. Sites for this species should possess good drainage. By contrast, *Rosa californica* appears to be much less sensitive to poor soil aeration and low soil nutrient availability; this species may grow well in a variety of microsites.

4) We would advise caution in application of summer water, at least as flood irrigation, for *Sambucus mexicana*. In our experiments, flood irrigation caused stress and mortality in this species when applied under conditions of high evaporative demand.

Within the guild of understory riparian species there are large differences in nutrient physiology and flooding tolerance. This is despite the fact that *Rosa californica* and *Sambucus mexicana* are both generally considered fast growing, high-nutrient-adapted species and are classified as "facultative" wetland species, i.e. equally likely to be found in wetland or upland sites. There is need for further documentation of this variation and incorporation of this information in restoration planning.

SUMMARY

Reestablishment of a diverse shrub understory as a component of riparian forests and woodlands is critical for biodiversity, wildlife habitat, and riparian vegetation functions including erosion resistance, and filtration of sediment, nutrients and contaminants. *Rosa californica* (California rose) and *Sambucus mexicana* (Blue elderberry) were selected for study as they are found throughout the California Central Valley in several widespread riparian vegetation types. In addition, blue elderberry is a host species for the threatened Valley elderberry longhorn beetle (*Desmocerus californicus dimorphus*). Field and greenhouse studies were conducted to provide basic understanding of establishment requirements and understanding of the nutrient dynamics of the species and ecosystem.

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Source of Variation	F value and significance level							
	20 Nov 92-19 Mar 93				19 Mar-28 May 93			
	df	R CANV	df	S CANV	df	R CANV	df	S CANV
Between subjects								
Block	7	1.18 ns	7	18.94 ****	7	2.01 ns	7	3.04 ns
preN	1	2.72 ns	1	3.92 ns	1	0.25 ns	1	0.57 ns
postNPK	1	2.55 ns	1	6.92 **	1	31.76 ***	1	6.88 **
preN* postNPK	1	0.73 ns	1	0.01 ns	1	3.72 ns	1	0.22 ns
Error(BSE)	21		19		21		19	
Within subjects						H-F		H-F
time (t)	1	0.19 ns	1	169.4 ****	5	4408.2 ****	5	143.12 ****
time* block	7	2.00 ns	7	11.17 ****	35	3.22 ***	35	5.51 ****
time* preN	1	0.04 ns	1	1.52 ns	5	0.78 ns	5	0.43 ns
time* postNPK	1	38.80 ****	1	10.46 **	5	12.25 ***	5	1.17 ns
t*preN* postNPK	1	0.94 ns	1	0.35 ns	5	4.86 **	5	1.31 ns
Error(WSE)	21		19		105		95	

Table 2. Relative growth rates (RGR), field experiment. These values were calculated using RGR variables, by treatment means for comparison of canopy volume-RGR from transplant to 19 March, and between harvests (19 March - 28 May) for canopy volume-RGR, plant biomass-RGR, and leaf area-RGR.
A: *Rosa californica* **B:** *Sambucus mexicana*

A ***Rosa californica*** Relative Growth Rates per day

	Canopy volume-RGR		Biomass-RGR	Leaf Area-RGR
preN/postNPK	20Nov-19Mar	19Mar-28May	19Mar-28May	19Mar-28May
high/high	0.0007	0.0266	0.0305	0.0385
low/high	0.0010	0.0288	0.0325	0.0451
high/low	-0.0009	0.0269	0.0282	0.0410
low/low	-0.0011	0.0258	0.0250	0.0350

B ***Sambucus mexicana*** Relative Growth Rates per day

	Canopy volume-RGR		Biomass-RGR	Leaf Area-RGR
preN/postNPK	20Nov-19Mar	19Mar-28May	19Mar-28May	19Mar-28May
high/high	-0.0073	0.0256	0.0157	0.0357
low/high	-0.0065	0.0247	0.0162	0.0339
high/low	-0.0144	0.0276	-0.0015	0.0229
low/low	-0.0155	0.0233	-0.0075	0.0469

Source of Variation	F value and significance level df	F	H-F
Between subjects			
block	4	9.41	****
species	1	53.38	****
preN	1	6.34	*
species*preN	1	0.91	ns
postN	2	21.22	****
species*postN	2	1.42	ns
preN*postN	2	1.56	ns
species*preN*postN	2	2.53	ns
Error(BSE)	44		
Within subjects			
time	8	250.23	****
time*block	32	0.72	ns
time*species	8	10.27	****
time*preN	8	5.46	**
time*species*preN	8	0.84	ns
time*postN	16	62.05	****
time*species*postN	16	9.26	****
time*preN*postN	16	0.85	ns
time*species*preN*postN	16	1.32	ns
Error(WSE)	352		

Table 4. Plant biomass, greenhouse 15N transplant experiment. ***A*** This is an analysis of variance of plant biomass (ln g) at the final harvest (28 d) with a combined preN and postN variable. Significance levels are: ns non-significant; * p<0.05; **p<0.01; *** p<0.001; **** p<0.0001. ***B*** Treatment means are presented as backtransformed mean biomass (g). Mean separation for treatment combinations by REGWF, on separate ANOVAs for each species. Values underlined by a single bar are not significantly different.

A Source of Variation	F value and significance level		
	df	F	
block	4	14.13	****
species	1	136.30	****
preNpostN	5	6.11	****
species*preNpostN	5	0.62	ns

B Biomass by species and treatment combination

	high/high	low/high	high/mod	high/low	low/mod	low/low
Rosa californica	4.93	4.59	4.29	3.72	3.66	3.19
Sambucus mexicana	3.90	3.03	2.97	2.42	2.28	1.97

Table 5. Mortality, greenhouse flooding experiment. Eight plants were in each treatment group. Values shown are percentage dead by the end of the experiment (1 March; see Figure 2).

	Flooding duration		
Species	0 weeks	4 weeks	8 weeks
Rosa californica	0 %	0 %	12.5 %
Sambucus mexicana	0 %	25 %	50 %

Figure 1. Timeline, greenhouse ^{15}N transplant experiment. Plants were initially grown in 1/4 strength modified complete nutrient solution (4 mM nitrogen) with no ^{15}N enrichment. Labelling with ^{15}N isotope (26.7 atom % ^{15}N) was initiated when seedlings were 12 weeks old, and continued until transplant. The treatments were varying nitrogen levels: the pretreatment was high (4 mM N) and low (0.2 mM N) nitrogen, the post-transplant treatments were three levels of nitrogen (4, 1.6, and 0.2 mM N).

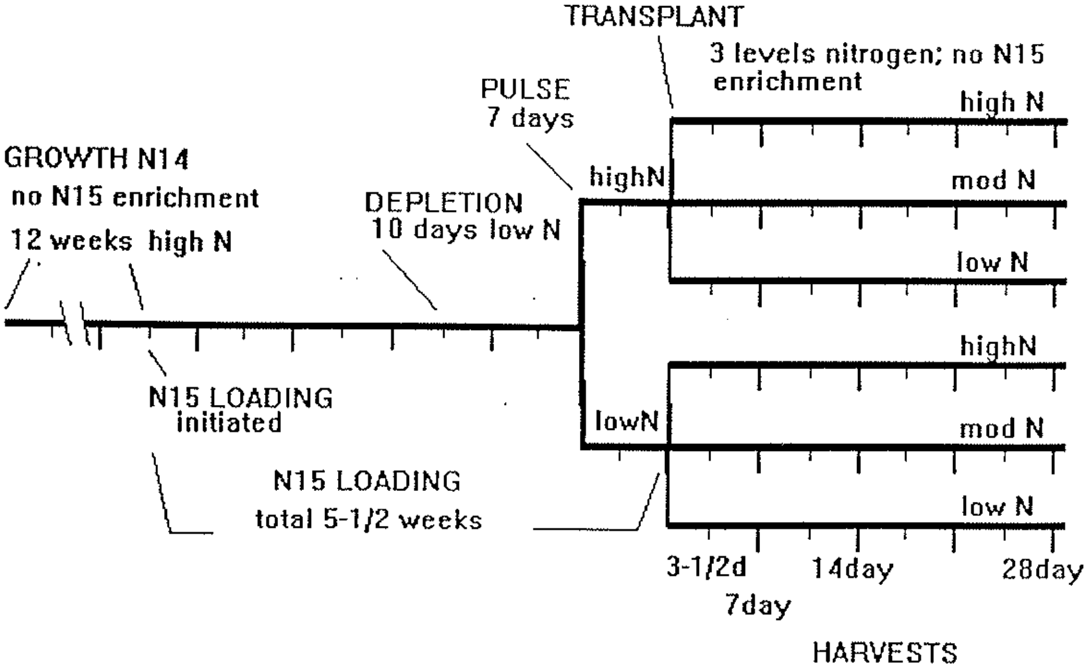
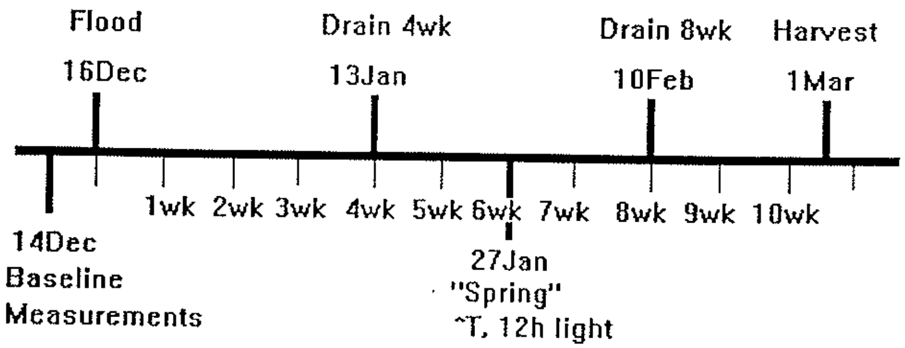
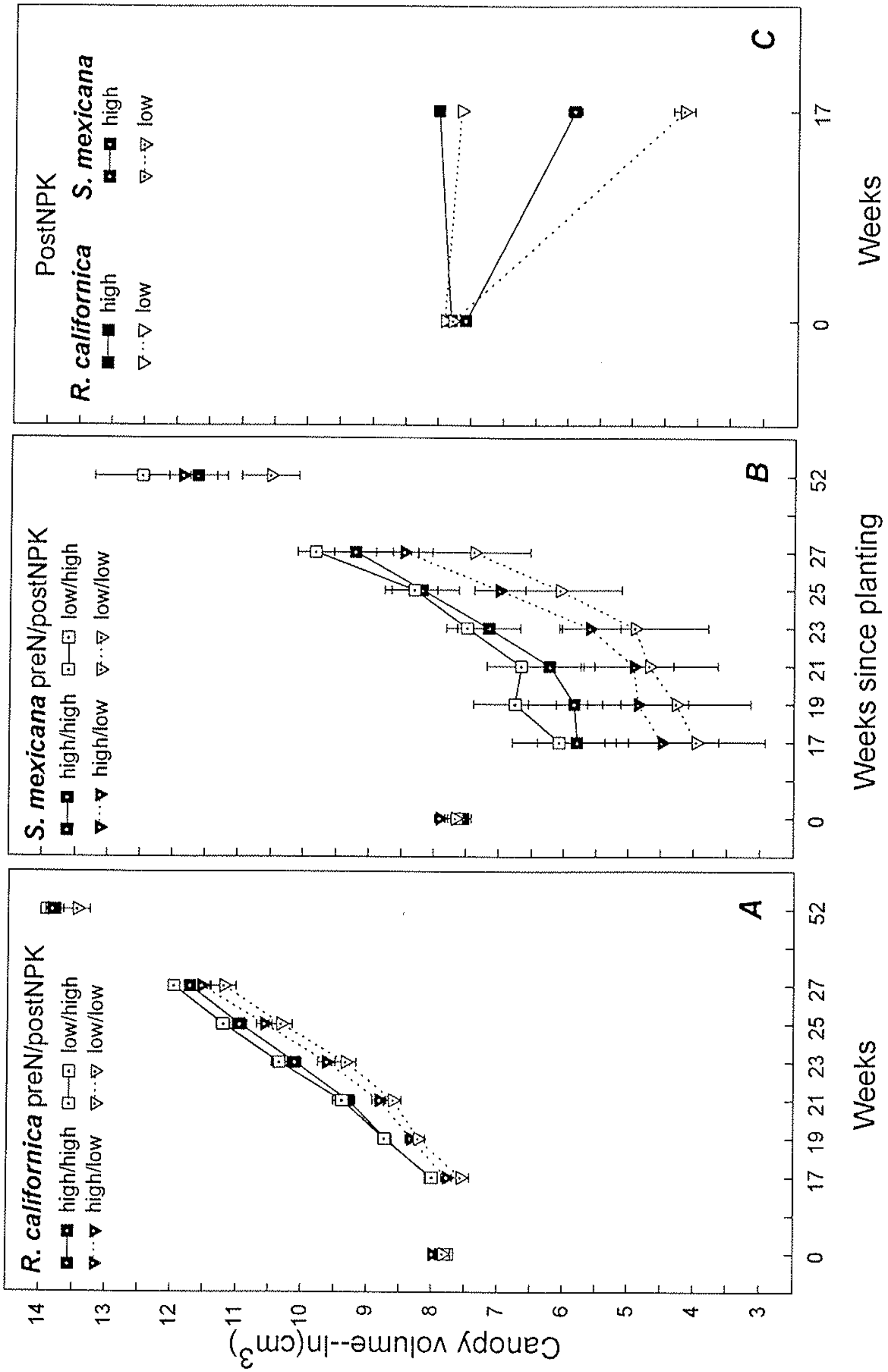
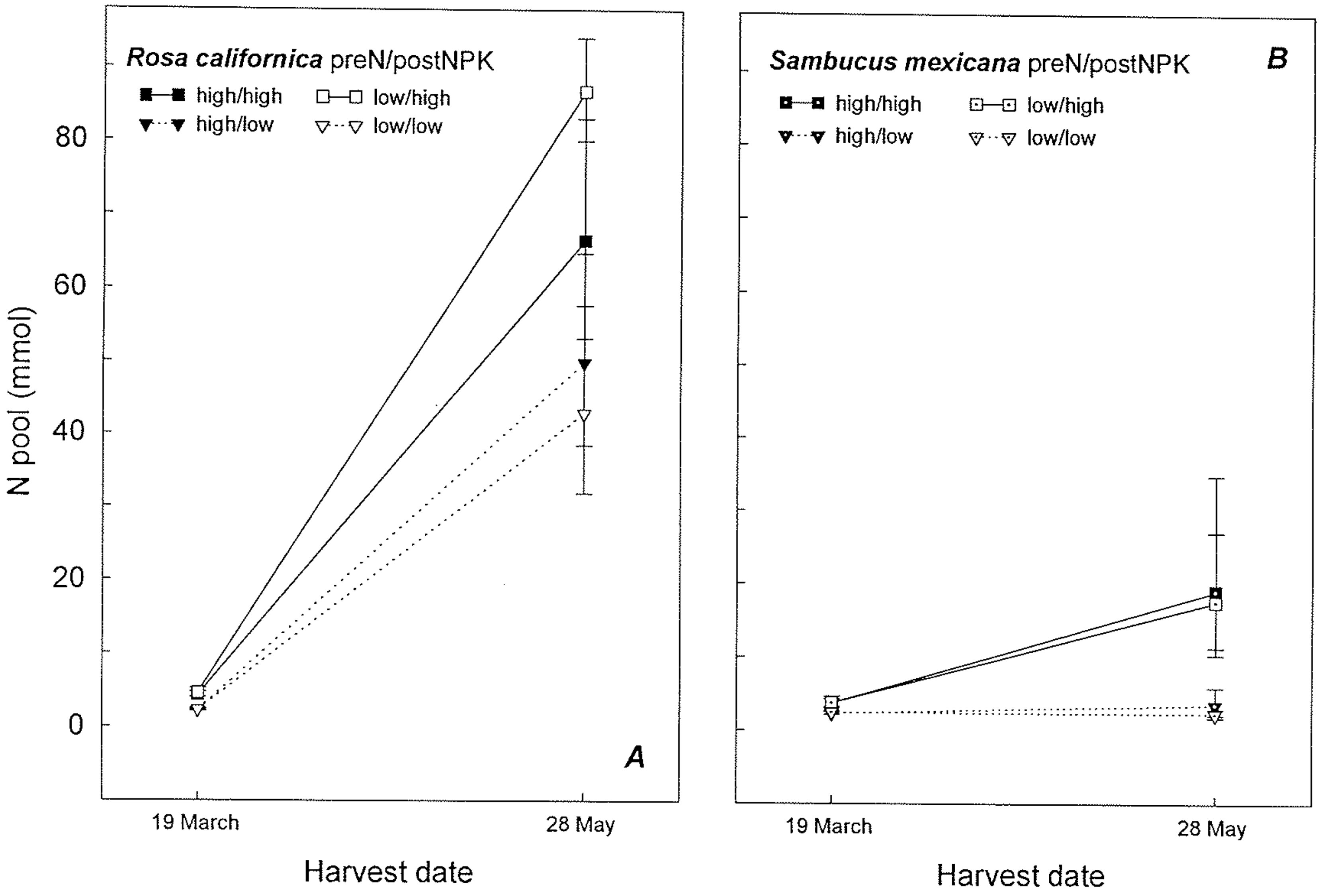


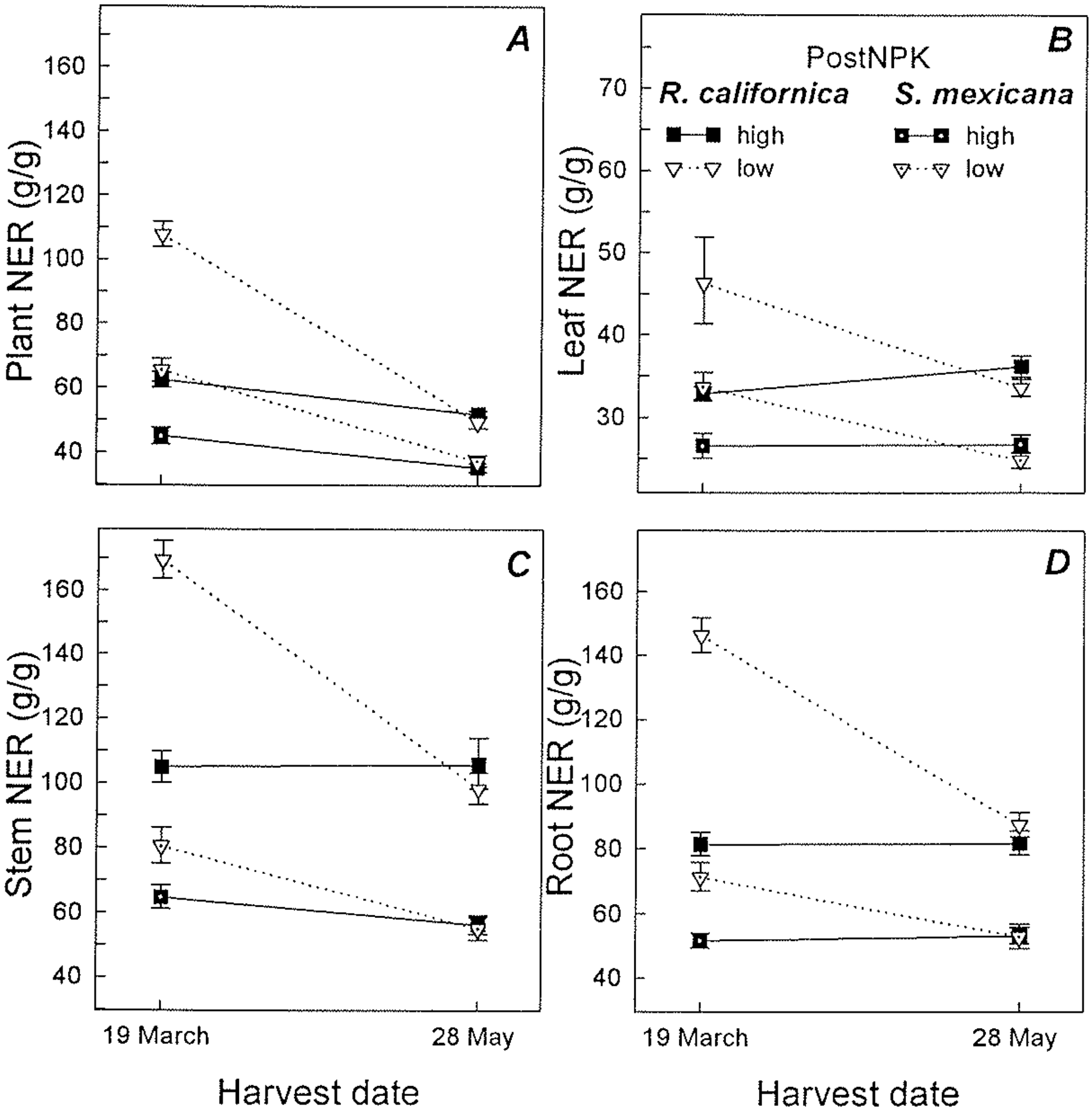
Figure 2. Timeline, greenhouse flooding experiment. The baseline measurements were used for a covariate. Flooded plants were inundated to 1-3cm above soil surface, and maintained for 4 or 8 weeks. Supplemental lighting 12 hours each day and increased temperature simulated spring to encourage growth, and would be expected to be more stressful for plants still flooded. All plants were harvested 1 March, 1993.

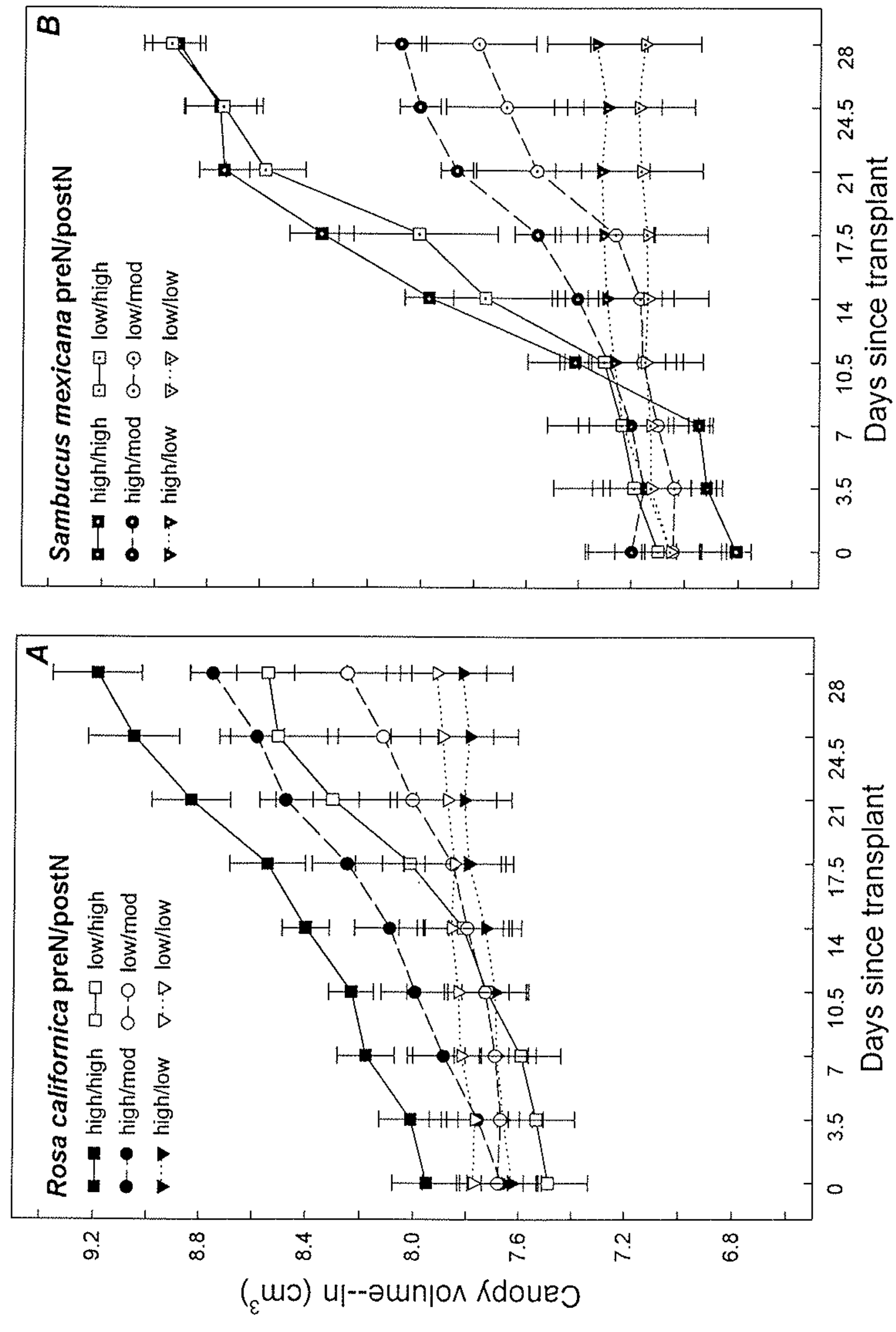


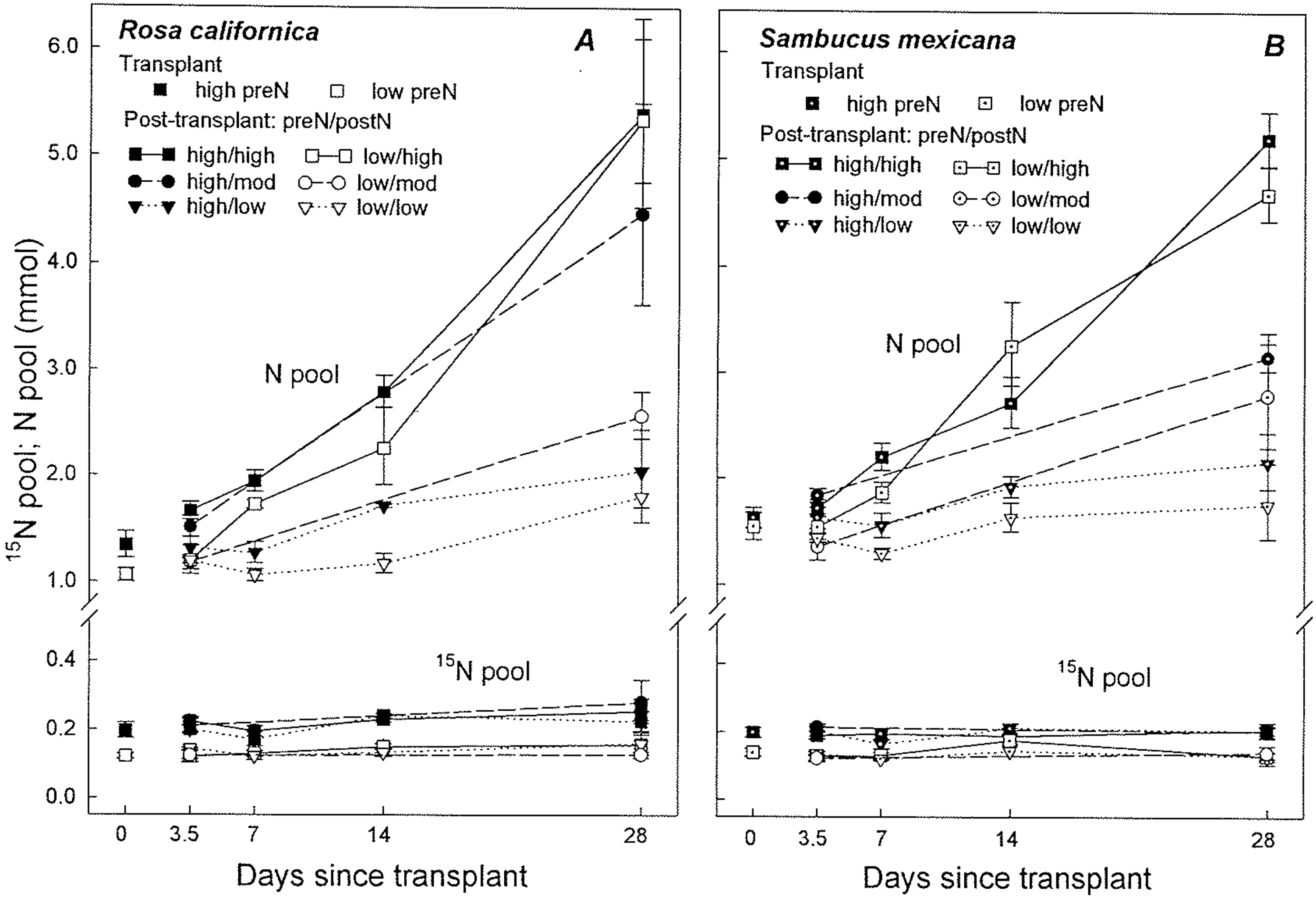

R. californica preN/postNPK
high/high
low/high
high/low
low/low
Weeks
A
S. mexicana preN/postNPK
high/high
low/high
high/low
low/low
Weeks since planting
B
PostNPK
R. californica
high
low
S. mexicana
high
low
Weeks
C
Canopy volume--ln(cm³)
14
13
12
11
10
9
8
7
6
5
4
3
0
17
19
21
23
25
27
52

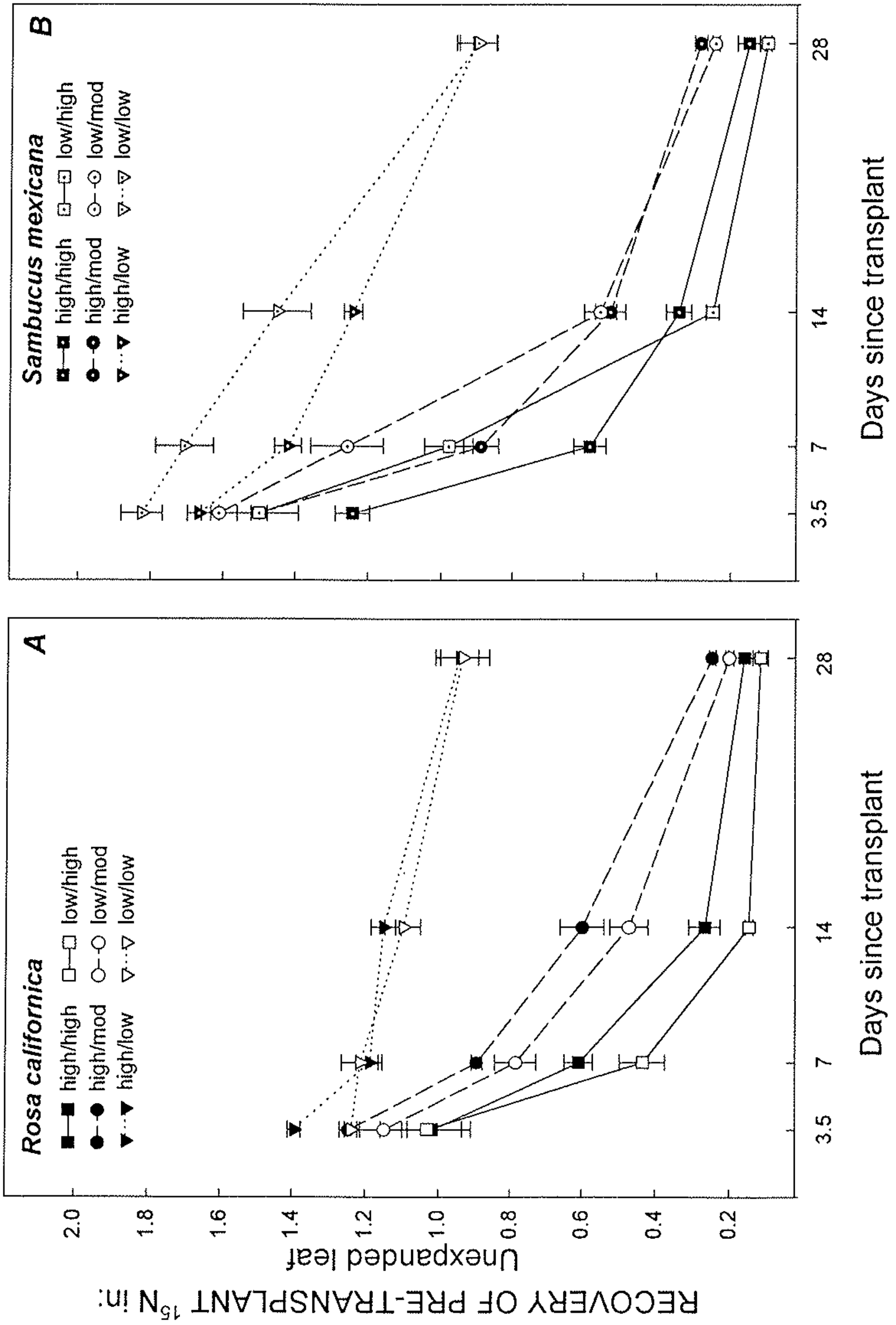


Rosa californica preN/postNPK
high/high
low/high
high/low
low/low
N pool (mmol)
80
60
40
20
0
A
19 March
28 May
Harvest date
Sambucus mexicana preN/postNPK
B
high/high
low/high
high/low
low/low
19 March
28 May
Harvest date


A
B
C
D
PostNPK
R. californica
S. mexicana
high
low
high
low
Plant NER (g/g)
Leaf NER (g/g)
Stem NER (g/g)
Root NER (g/g)
160
140
120
100
80
60
40
70
50
30
19 March
28 May
Harvest date
Harvest date


A
Rosa californica preN/postN
high/high
low/high
high/mod
low/mod
high/low
low/low
B
Sambucus mexicana preN/postN
high/high
low/high
high/mod
low/mod
high/low
low/low
Canopy volume--ln (cm^3)
9.2
8.8
8.4
8.0
7.6
7.2
6.8
0
3.5
7
10.5
14
17.5
21
24.5
28
Days since transplant


Rosa californica
A
Transplant
high preN
low preN
Post-transplant: preN/postN
high/high
high/mod
high/low
low/high
low/mod
low/low
N pool
^{15}N pool
^{15}N pool; N pool (mmol)
6.0
5.0
4.0
3.0
2.0
1.0
0.4
0.2
0.0
0
3.5
7
14
28
Days since transplant
Sambucus mexicana
B
Transplant
high preN
low preN
Post-transplant: preN/postN
high/high
high/mod
high/low
low/high
low/mod
low/low
N pool
^{15}N pool
0
3.5
7
14
28
Days since transplant


A
Rosa californica
high/high
high/mod
high/low
low/high
low/mod
low/low
B
Sambucus mexicana
high/high
high/mod
high/low
low/high
low/mod
low/low
RECOVERY OF PRE-TRANSPLANT ^{15}N in:
Unexpanded leaf
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
3.5
7
14
28
Days since transplant
Days since transplant

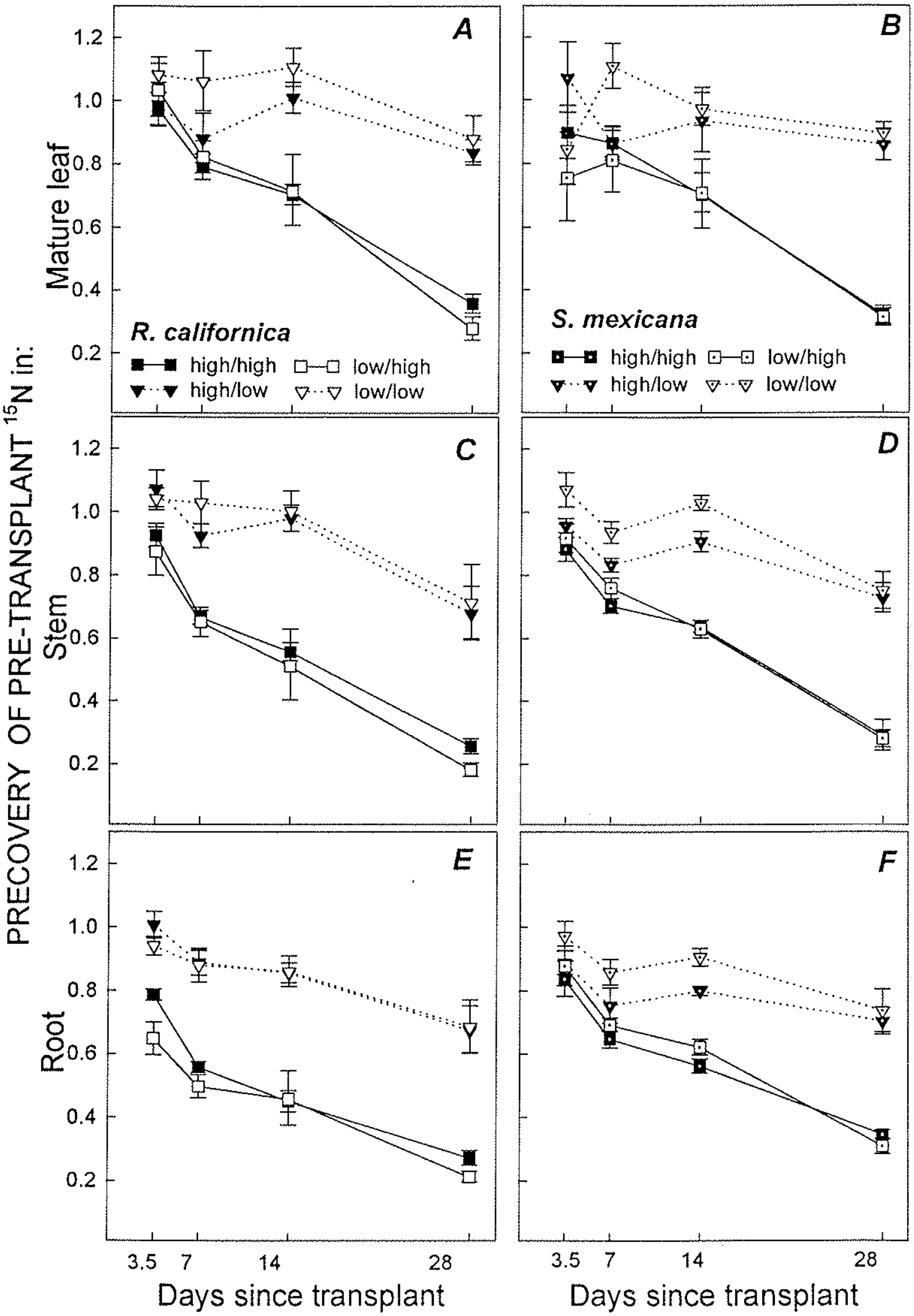

A
B
C
D
E
F
Mature leaf
Stem
Root
PRECOVERY OF PRE-TRANSPLANT ^{15}N in:
R. californica
S. mexicana
high/high
low/high
high/low
low/low
1.2
1.0
0.8
0.6
0.4
0.2
3.5
7
14
28
Days since transplant
Days since transplant

Figure 11. Canopy volume, greenhouse flooding experiment. These are the canopy volumes (ln cm^3) at the conclusion of 8 weeks of inundation for long-flooded plants (see Figure 2). Short-flood plants had been drained for 4 weeks, and all had been exposed light and temperatures to stimulate growth for 2 weeks. The initial values for each treatment were measurements taken prior to flooding, and were used as a covariate in the analysis of variance.