*Ecology*, 88(5), 2007, pp. 1328–1334


# EFFECT OF ELEVATED $CO_2$ ON COARSE-ROOT BIOMASS IN FLORIDA SCRUB DETECTED BY GROUND-PENETRATING RADAR

Daniel B. Stover,[1,4] Frank P. Day,[1] John R. Butnor,[2] and Bert G. Drake[3]

[1]*Department of Biological Sciences, Old Dominion University, Norfolk, Virginia 23529 USA*
[2]*U.S. Forest Service, Southern Research Station, Research Triangle Park, North Carolina 27709 USA*
[3]*Smithsonian Environmental Research Center, Edgewater, Maryland 21037 USA*

*Abstract*. Growth and distribution of coarse roots in time and space represent a gap in our understanding of belowground ecology. Large roots may play a critical role in carbon sequestration belowground. Using ground-penetrating radar (GPR), we quantified coarse-root biomass from an open-top chamber experiment in a scrub-oak ecosystem at Kennedy Space Center, Florida, USA. GPR propagates electromagnetic waves directly into the soil and reflects a portion of the energy when a buried object is contacted. In our study, we utilized a 1500 MHz antenna to establish correlations between GPR signals and root biomass. A significant relationship was found between GPR signal reflectance and biomass ($R^2 = 0.68$). This correlation was applied to multiple GPR scans taken from each open-top chamber (elevated and ambient $CO_2$). Our results showed that plots receiving elevated $CO_2$ had significantly ($P = 0.049$) greater coarse-root biomass compared to ambient plots, suggesting that coarse roots may play a large role in carbon sequestration in scrub-oak ecosystems. This nondestructive method holds much promise for rapid and repeatable quantification of coarse roots, which are currently the most elusive aspect of long-term belowground studies.

*Key words: carbon dioxide; coarse-root biomass; ground-penetrating radar; roots; scrub oak.*

## Introduction

Atmospheric carbon dioxide ($CO_2$) has been increasing in concentration globally over the past century and current biosphere models predict $CO_2$ concentration will double within the next 50–100 years to ~700 ppm with a likely mean global temperature increase of 1.4–5.8°C (Schlesinger 1991, IPCC 2001). It is unclear how plant communities will respond to this change in $CO_2$ concentration. However, many studies suggest changes in species dominance, resource availability and allocation, invasiveness, and, most importantly, alteration of ecosystem services (Ward and Strain 1999, Korner 2001, Bazzaz and Catovsky 2002, Poorter and Navas 2003). Belowground responses have traditionally been ignored or oversimplified (Mooney 1991, Mooney et al. 1991, Korner and Arnone 1992, Day et al. 1996). The allocation of carbon to the root system has implications for long-term sequestration and storage of excess atmospheric $CO_2$ in the rhizosphere (Pregitzer et al. 1995, Johnston et al. 2004, Day et al. 2006).

Long-term data from an elevated $CO_2$ experiment on Merritt Island at Kennedy Space Center, Florida indicate that fine root growth was higher during the initial years of elevated $CO_2$ treatment (postburn) (Dilustro et al. 2002). However, as the community matured, the $CO_2$ treatment effect appears to have disappeared (Day et al. 2006). In addition, we have suggested that this system has reached root closure (i.e., carrying capacity) in the fine root component of belowground biomass (Day et al. 2006). We know little about effects on larger underground plant structures. Coarse roots and other large belowground structures have been underrepresented in most studies (Norby 1994), but are expected to play a critical role in regrowth in the scrub-oak ecosystems, which are fire controlled with a 7–15 year natural burn cycle (Schmalzer and Hinkle 1991).

Historically, root systems have been the most understudied aspect of plant biology (Waisel et al. 2002). This is due to the opaque nature of soils and difficulties in repeatability of quantitative measures of root systems (Fitter and Stickland 1992, Nielsen et al. 1997). Most root quantification methods, such as in-growth cores, soil cores, and pits are destructive, thus hindering repeated assessments in long-term studies (Norby and Jackson 2000, Pierret et al. 2005). In addition, these methods are often labor intensive and limited by manageability of size and number of samples. Nondestructive root analysis methods, such as mini-rhizotron tubes, only elucidate the fine roots within the

Manuscript received 9 June 2006; revised 20 October 2006; accepted 9 November 2006. Corresponding Editor: S. D. Smith.
[4] E-mail: dstover@odu.edu

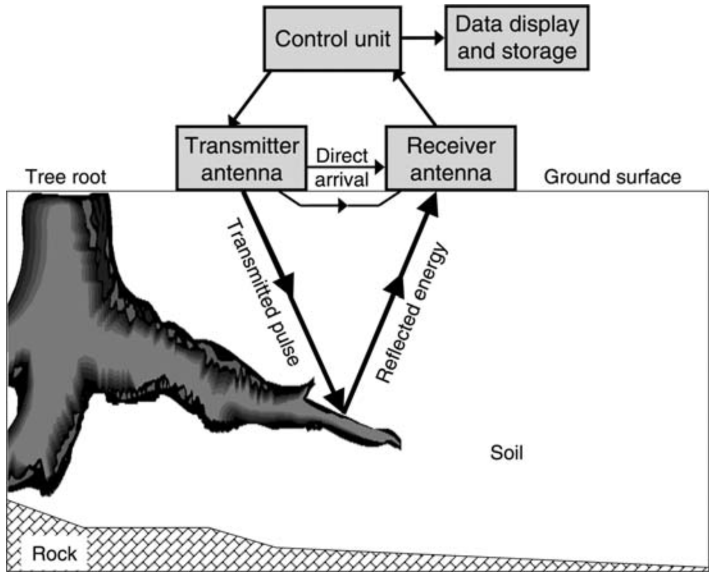


FIG. 1. Basic ground-penetrating radar (GPR) operation. High-frequency electromagnetic waves are emitted from the transmitting antenna complex into the soil and reflect off a buried object back to the receiving antenna. Time and signal strength are recorded by the control unit and produce hyperbolic-shaped images on the display screen.

system (Hendrick and Pregitzer 1992). A major gap in our current understanding of root systems involves coarse roots and other large belowground structures.

Ground-penetrating radar (GPR) is a 30-year-old geophysical technique that pulses ultra high-frequency (~100–1500 MHz) electromagnetic waves into the ground (Wielopolski et al. 2000, Daniels 2004). Electromagnetic waves travel through the soil and reflect off buried objects, such as roots, back to a receiving antenna (Fig. 1). The GPR control unit measures the intensity and velocity of the signal along with the propagation time (Hruska et al. 1999). GPR technology holds promise for quantifying root mass and architecture due to its rapid, nondestructive acquisition of data (~90-ns collection time per scan; Butnor et al. 2001). Recent studies with GPR using a 1500-MHz frequency antenna have distinguished roots with diameters as small as 0.5 cm (Butnor et al. 2001).

The goal of this study was to apply GPR technology to questions pertaining to the influence of elevated $CO_2$ on coarse roots in a scrub-oak ecosystem at Kennedy Space Center, Florida. We established a relationship between GPR signal strength and root biomass. Using this relationship, we estimated coarse-root biomass in open-top chambers in an elevated $CO_2$ experiment where destructive measurements cannot be performed. We hypothesized that scrub oak that has been continually fumigated with elevated $CO_2$ would have greater coarse-root biomass than plants exposed to ambient $CO_2$ concentrations.

## METHODS

### *Site description*

The study site for this research is located on Merritt Island in Brevard County, Florida, USA (28°36′29″ N; 80°40′15″ W). Merritt Island, located on the northern part of Kennedy Space Center (KSC), is a subtropical barrier island with topography ranging from sea level to ~2 m above mean sea level (Huckle et al. 1974, Mailander 1990).

The soils are primarily sandy and dominated by the Pomello soil type. Pomello is a moderately well-drained Spodosol (Aernic Haplahumod) derived from deposited marine sands (Huckle et al. 1974, Baldwin et al. 1980, Schmalzer and Hinkle 1987). Soils located at our site are typically acidic (pH 3–4), nutrient poor (most notably nitrogen limited), and low in organic matter content. GPR is best suited for dry sandy conditions; wet or high clay content soils usually exhibit signal attenuation, resulting in diminished resolution for accurate interpretation (Doolittle et al. 2002, Leckebusch 2003, Daniels 2004). Doolittle et al. (2002) mapped relative soil suitability for GPR work for the conterminous United States.

The scrub-oak community is primarily composed of *Quercus myrtifolia* Wasd. (76%), *Quercus geminata* Small (15%), *Quercus chapmanii* (7%), *Serenoa repens* (Bartram) Small, and *Lyonia ferruginea* (Walt.) Nutt. These scrub communities are historically fire-controlled with a natural 10–15 year fire cycle (Schmalzer and Hinkle 1991, 1992). Our study site was control burned in February 1996 before treatments were initiated. The scrub-oak ecosystem was selected because it represents a perennial, subtropical woody community with high evaporative demand and low nutrient availability (Day et al. 1996).

### *$CO_2$ treatment*

Open-top chambers (OTCs) were used to create elevated $CO_2$ environments (Drake et al. 1989). A total of 16 chambers were fabricated with PVC frames covered with clear mylar sheeting. Each octagonal chamber was designed with sides of 139.9 cm, a maximum diameter of 356.6 cm, and a height of 365 cm. Treatments were initiated following a controlled burn of the system. Blocks (consisting of one representative from each elevated and ambient treatment) were assigned according to similarity of preexisting vegetation composition ($N = 8$ chambers per treatment). Carbon dioxide treatments initiated on May 1996 and continually treated to date, include eight ambient (~350 ppm $CO_2$) chambers and eight elevated (~700 ppm $CO_2$) chambers. This represents >10 years of continuous $CO_2$ fumigation. Carbon dioxide treatments are applied with a continuous air circulation system 24 hours a day.

### *Root biomass cores*

In June 2005 and September 2006, 30 soil core locations were selected in the scrub-oak community adjacent to the chambers. Prior to coring, each core location was scanned with a Subsurface Interface Radar System (SIR-3000) attached to a model 5100 (1500 MHz) GPR antenna (Geophysical Survey Systems, North Salem, New Hampshire, USA). Other studies have found a frequency trade-off between depth of penetration and resolution (Hruska et al. 1999, Cox et al. 2005). Low-frequency antennas (i.e., 400 MHz) penetrate deeper into the soil but have a low ability to resolve detailed objects. High-frequency antennas are smaller and tend to be better at resolving detailed objects, but are limited to a depth <1 m. Prior to fieldwork, the radar unit was scaled for depth by determining the average dielectric constant of the soil with a buried metallic object at a known depth (similar to Butnor et al. 2003). Each coring location was scanned with the centerline of the antenna moving 15 cm in length. Once the GPR data were collected, a 15 cm diameter corer was used to extract a soil core to a depth of 60 cm. Each core was divided into three 20-cm segments, which were dry sieved, refrigerated, separated one week later into live, dead (based on lack of flexibility and loss of structural integrity), and unidentifiable organic matter fractions, and dried at 70°C for 48 hours before weighing. Larger roots were dried longer until there was no change in mass after 24 hours. Large rhizomes, burls (lignotubers), and belowground stems are extremely common in scrub-oak ecosystems; thus, we classified any belowground structures >5 mm diameter as coarse roots.

### *GPR image processing and root biomass correlations*

Core location scans were processed with RADAN 6.5 GPR data processing software (Geophysical Survey Systems, North Salem, New Hampshire, USA). Each individual scan was cropped to ensure that only the actual 15 cm area of the core was analyzed. Before quantification of the scans, several data processing steps were applied to enhance root discrimination. Root structures appear as hyperbolic reflectors, whereas parallel bands represent plane reflectors such as ground surface, soil layers, and low-frequency noise (Fig. 2). Parallel bands were removed with a horizontal finite impulse response filter (FIR) filtration method called background removal (Oppenheim and Schafer 1975, Butnor et al. 2003). We used the Kirchoff migration to correct the position of objects and collapse hyperbolic diffractions based on signal geometry (Daniels 2004). Finally, we performed a Hilbert transformation on the radar data. Hilbert transformations express the relationship between magnitude and the phase of the signal allowing the phase of the signal to be reconstructed from its amplitude, thus allowing subtle properties and objects to be elucidated and reducing false "echoes" (Oppenheim and Schafer 1975, GSSI 2004). Radar profiles were converted to bitmap image files using Radan to Bitmap Conversion Utility 1.4 (Geophysical Survey Systems, North Salem, New Hampshire, USA).

Radar images were quantified with Sigma Scan Pro Image Analysis software (Systat 2004). Each image was converted to an 8-bit gray scale image. To quantify roots within the image, pixel intensity was measured (Cox et al. 2005). Intensity is a relative measure of how light or dark an individual pixel is on a scale of 0 (black) to 255 (white). We used an intensity threshold range of 60–255 pixels, which was able to delineate roots >0.5 cm. This technique measures the relative pixel area of interest (Cox et al. 2005). Past studies suggest that large diameter dead roots will persist for substantial periods of time in the soil matrix and therefore should be combined with live roots to estimate total belowground biomass (Butnor et al. 2005, Cox et al. 2005). Therefore, a linear regression was performed to quantify the relationship between total root biomass (live and dead) from the soil cores and the GPR signals (pixels within the threshold range).

### *Root biomass in chambers*

In December 2005, five stratified-random GPR scans were taken within each of the 16 open-top chambers (eight ambient and eight elevated). There were restrictions on sample locations due to installed instruments and sampling devices, and the space occupied by plant stems could not be scanned. Each scan was 15 cm long and was processed in RADAN and Sigma Scan in the same manner as the core location scans previously

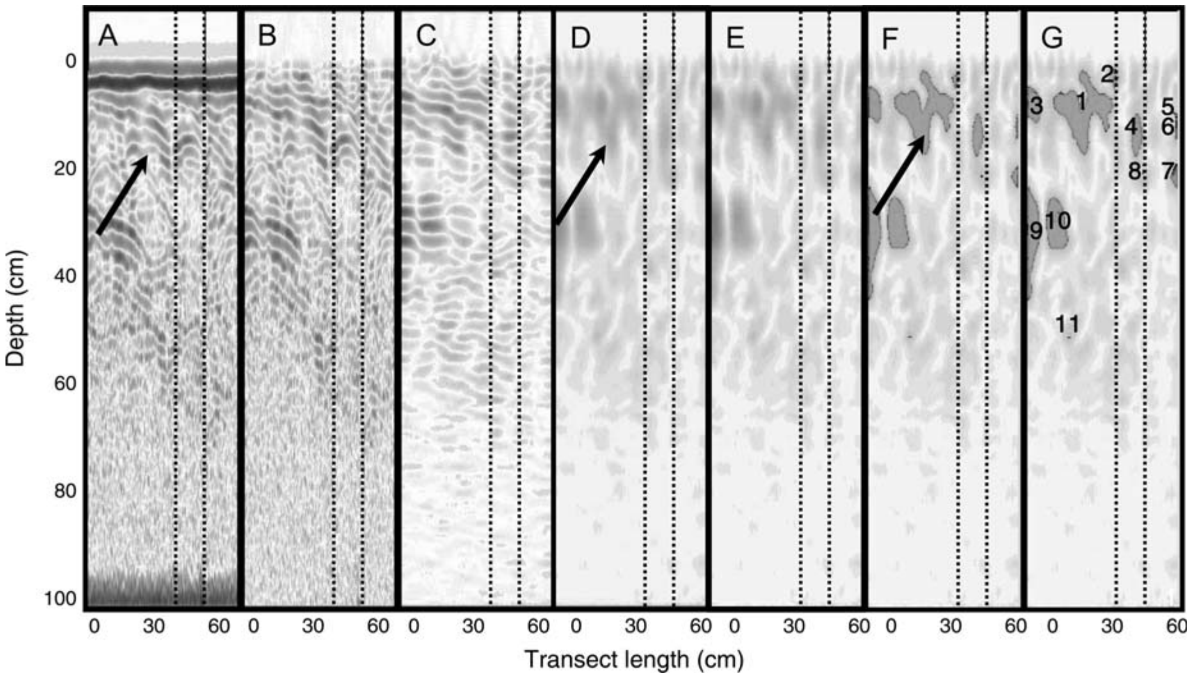


FIG. 2. Representative radar profile and standard image analysis/processing from a scrub-oak ecosystem at Kennedy Space Center, Florida, USA. Arrows point to a common reflector (i.e., root) located at 15 cm depth. Dotted vertical lines show the relative size for an individual core that would be extracted for biomass correlation. (A) Raw radar data from a 1500-MHz ground-penetrating radar antenna; (B) same profile processed in RADAN software with a finite impulse response filter (FIR) background removal to reduce low-frequency noise and bands; (C) Kirchoff migration, used to correct the reflector's (object's) position and hyperbolic geometry; (D) radar profile after a Hilbert transformation to express the magnitude of the signal to enhance the subtle objects and reduce false "echoes"; (E) post-processed images converted to gray scale; (F) roots quantified with Sigma Scan Pro Image Analysis software by setting the image pixel intensity threshold to the 60–255 range, which measures each pixel's intensity on a threshold scale; and (G) quantification of the image, accomplished by summing the number of pixels in each grouping (given a unique number).

described. The sum of each scan's intensity threshold was used to estimate biomass with the regression equations developed from the biomass cores. The effects of $CO_2$ enrichment on coarse-root biomass were tested by ANOVA using the MIXED procedure in SAS (SAS Institute 1990). Within our statistical model, biomass was blocked within chamber and $CO_2$ was the fixed effect.

## RESULTS

### *Root biomass/GPR regressions*

Biomass from the cores was partitioned into live and dead roots (Table 1). The average live biomass was 290 g (15 395 g/m$^2$) and the average dead biomass was 44 g (2308 g/m$^2$). Mean total biomass in the cores was 331 g/core (17 703 g/m$^2$). Root diameters varied among cores, but large diameter roots were captured by the 15-cm core. Roots and other belowground structures with the largest diameters (7.9–15 cm) were primarily found in the top 20 cm of the soil profile. A noticeable decline in diameter size was observed with increasing depth. At the 40–60 cm depth, the largest roots measured ~2–5 cm diameter. The regression between root biomass (live plus dead components) and the total number of pixels within the thresholds from the GPR images yielded a significant relationship ($R^2 = 0.68$; $r = 0.822$; Fig. 3).

TABLE 1. Root core dry mass (g/15 cm diameter core) ranges for different root fractions to 60 cm depth.

| Root fraction | Root core dry mass (g/core) | | | Biomass (g/m$^2$) |
|---|---|---|---|---|
| | Max. | Min. | Mean ± SE | Mean ± SE |
| Live | 1696 | 45 | 290 ± 68 | 15 395 ± 3717 |
| Dead | 82 | 18 | 44 ± 3 | 2308 ± 174 |
| Total | 1728 | 62 | 331 ± 69 | 17 703 ± 3762 |

### *Root biomass in chambers*

The regression equation was applied to GPR scans from the open-top chambers. Root biomass in the elevated and ambient chambers was estimated at 8971 ± 1105 g/m$^2$ (mean ± SE) and 6551 ± 1295 g/m$^2$, respectively (Fig. 4). There was a significant $CO_2$ treatment effect for coarse-root biomass in the scrub-oak system ($P = 0.049$). The effects of soil moisture on GPR signal penetration were examined at our field site

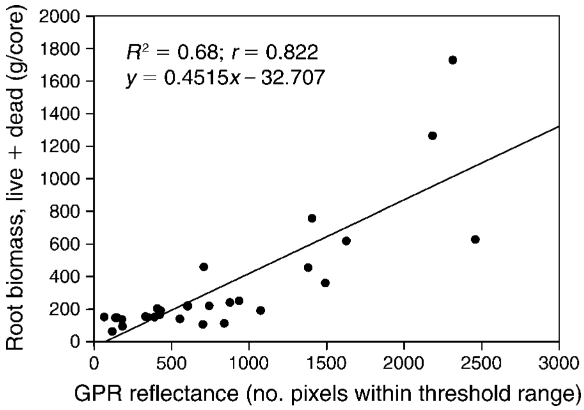


FIG. 3. Relationship between total live plus dead root biomass obtained from soil cores (g/15 cm core diameter to 60 cm depth) and ground-penetrating radar (GPR) root reflectance (total pixels within threshold). Root reflectance was determined by measuring the total number of pixels (pixel intensity) within a specific intensity threshold in each GPR image. The solid line represents a significant linear regression of the mass to GPR signal reflectance.

by scanning multiple locations following the addition of increasing amounts of water. Soil moisture was recorded with a handheld TDR probe at 20 cm depth. The sandy soils at Merritt Island drain rapidly, thus producing little change in our interpretation of scans except in the case of saturated field moisture conditions (D. B. Stover, *unpublished data*). As a result, we feel confident that our results from GPR data interpretation and predictive root biomass equations are not limited to just conditions present at the time of core collection.

## DISCUSSION

The goal of this study was to apply recent advances in ground-penetrating radar to the difficult determination of belowground effects of elevated $CO_2$ in a long-term study. The results indicate that properly processed GPR data can reasonably detect root biomass in the upper 60 cm of the soil profile. Significant relationships between the combined live and dead coarse-root biomass and the total number of pixels within the radar image provide a basis for a robust measurement of root biomass.

Processed GPR data applied to our biomass regression equation showed significantly different biomass between $CO_2$ treatments, indicating that scrub oak treated with elevated $CO_2$ had more coarse-root biomass than areas treated with ambient atmospheric $CO_2$. This implies that more carbon sequestration is occurring in elevated $CO_2$ chambers in the form of coarse roots. Belowground carbon storage in the coarse roots probably plays an important role in the regrowth of the scrub-oak community following fire. It is estimated that roots can comprise 40–85% of net primary production in some ecosystems (Fogel 1985, Fitter 1987). Norby et al. (1993) and Norby (1994) implied the importance of examining $CO_2$ effects on *Quercus* because root mass increased more than twice that of stem mass. These studies showed 77–136% increase in root mass in *Q. alba* grown under elevated compared to ambient $CO_2$. The ecosystem in the current study is dominated by scrub oaks and saw palmetto, which are clonal and produce large amounts of coarse roots, lignotubers, and belowground stems. Sclerophyllous shrublands and tropical evergreen forests tend to produce the greatest total mass of roots, on average ~5 kg/m$^2$ (Jackson et al. 1996, Robinson et al. 2003). Large root burls are very common in this system, thus making it difficult to separate the belowground stem from the root system. These structures provide major carbohydrate storage for regrowth and are known to persist long after aboveground biomass is removed. These structures play a major role in postfire recovery and are a critical component of belowground storage and ecology in this shrub system.

Numerous studies (e.g., Norby 1994, Miller et al. 2006) have suggested that coarse roots are large carbon sequestration sites and predicted that greater biomass should be present in elevated $CO_2$ treatments, but few if any have been able to quantify this effect. Our finding provides support for these predictions. This finding is unique in that this study is one of the first to nondestructively quantify coarse roots as affected by elevated $CO_2$. The methods utilized in this study can be applied to long-term studies to refine our understanding of coarse roots as well as to examine changes in biomass of larger belowground structures over time.

Previous belowground studies at our site have focused only on fine roots via minirhizotron methodology (Day et al. 1996). Early in the study, a treatment effect was reported; however, after about three years, this effect had dissipated (Day et al. 2006). Many woody plants in fire-controlled systems develop large belowground structures. In this system, biomass is promoted in elevated $CO_2$ treatments and most notably in the

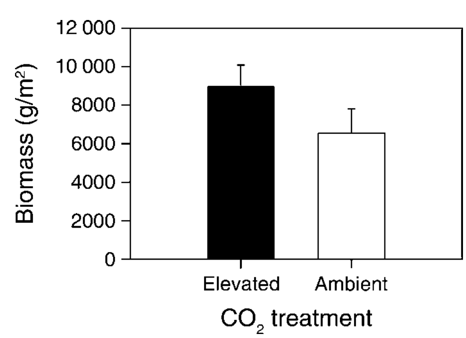


FIG. 4. Differences between coarse-root biomass under ambient and elevated $CO_2$ treatments (over 10 years of continual fumigation) estimated from ground-penetrating radar scans. Error bars represent +SE.

belowground component. Estimated aboveground biomass (leaves and stems combined) was 1362 $g/m^2$ in ambient treatments, whereas in the elevated treatments, aboveground biomass was ~2037 $g/m^2$ (e.g., Dijkstra et al. 2002; T. Seiler, *unpublished data*). Belowground, the ambient chambers had 6551 $g/m^2$ in coarse-root biomass whereas the elevated chambers had 8971 $g/m^2$. Fine root biomass comprised 2226 $g/m^2$ and 2203 $g/m^2$ in the ambient and elevated chambers, respectively (A. Pagel, *unpublished data*). Because the fine roots had apparently reached closure in both treatments, the increase in belowground biomass under elevated $CO_2$ was proportionally greater in coarse roots (75% ambient, 80% elevated) compared to the fine roots (25% ambient, 19% elevated). Based on the above and belowground estimates, total biomass was ~10 139 $g/m^2$ and 13 212 $g/m^2$ for ambient and elevated $CO_2$ treatments, respectively, thus indicating that the increase in biomass distributed under elevated $CO_2$ was distributed in the same proportion above and belowground as in the ambient treatments. The contribution of belowground biomass to system carbon storage was massive (85% of total biomass).

While using GPR for root analysis is still in its infancy, this technique shows great promise for elucidating belowground plant structures. Very few studies have applied GPR to biological systems, especially to roots. GPR based estimates require substantial ground-truthing to ensure accurate quantification and repeatability of the technique. Potential future applications of GPR to our system will focus on determining coarse-root growth patterns temporally (growth rates) and spatially (root architecture). Similar to other studies, our method only identifies roots greater than ~0.5 cm diameter (Wielopolski et al. 2000, Butnor et al. 2001, 2003, Cox et al. 2005). Therefore, this study excludes the fine root biomass component.

In conclusion, GPR based biomass estimates suggest elevated $CO_2$ chambers have greater belowground biomass, indicating a significant treatment effect in a scrub-oak ecosystem, thus supporting our central hypothesis. In addition, GPR appears to be a rapid and feasible method to quantify and examine coarse roots and is redefining our understanding of the role larger belowground structures play in ecosystem dynamics.


## Acknowledgments

This work was funded by subcontract (95-59-MPOOO02) to the Smithsonian Institution's grant from the U.S. Department of Energy (DE-FG-02-95ER61993). We thank Julie Ray, Christina Morgan, Chris Day, and Brad Carwile for field assistance and root core processing and Steven Schindler and Lori Jones for GPR permit assistance. We also appreciate biomass data provided by Troy Seiler and Alisha Pagel. We especially thank the U.S. National Aeronautical and Space Administration and Smithsonian site staff for providing continual support throughout the project.


## Literature Cited


Baldwin, R., C. L. Burch, R. B. Hinton, H. H. Huckle, P. Nichols, F. C. Watts, and J. A. Wolfe. 1980. Soil survey of Volusia County, Florida. USDA Soil Conservation Service, Washington, D.C., USA.

Bazzaz, F. A., and S. Catovsky. 2002. Impact of global environmental change on plants: from cells to ecosystems. Pages 94–111 *in* H. A. Mooney and J. G. Canadell, editors. Encyclopedia of global environmental change. Volume 2. Wiley, Chichester, UK.

Butnor, J. R., J. A. Doolittle, K. H. Johnsen, L. Samuelson, T. Stokes, and L. Kress. 2003. Utility of ground-penetrating radar as a root biomass survey tool in forest systems. Soil Science Society of America Journal 67:1607–1615.

Butnor, J. R., J. A. Doolittle, L. Kress, S. Cohen, and K. H. Johnsen. 2001. Use of ground-penetrating radar to study tree roots in the southeastern United States. Tree Physiology 21: 1269–1278.

Butnor, J., B. Roth, and K. Johnsen. 2005. Feasibility of using ground-penetrating radar to quantify root mass in Florida's intensively managed pine plantations. Forest Biology Research Cooperative Report Number 38. Gainesville, Florida, USA.

Cox, K. D., H. Scherm, and N. Serman. 2005. Ground-penetrating radar to detect and quantify residual root fragments following peach orchard clearing. HortTechnology 15: 600–607.

Daniels, D. J. 2004. Ground penetrating radar. Second edition. Institution of Electrical Engineers, London, UK.

Day, F. P., D. B. Stover, A. L. Pagel, B. A. Hungate, J. J. Dilustro, B. T. Herbert, B. G. Drake, and C.R. Hinkle. 2006. Rapid root closure after fire limits fine root responses to elevated atmospheric $CO_2$ in a scrub oak ecosystem in central Florida, USA. Global Change Biology 12:1047–1053.

Day, F. P., E. P. Weber, C. R. Hinkle, and B. G. Drake. 1996. Effects of elevated atmospheric $CO_2$ on fine root length and distribution in an oak–palmetto scrub ecosystem in central Florida. Global Change Biology 2:143–148.

Dijkstra, P., G. Hymus, D. Colavito, D. A. Vieglais, C. M. Cundari, D. P. Johnson, B. A. Hungate, C. R. Hinkle, and B. G. Drake. 2002. Elevated atmospheric $CO_2$ stimulates aboveground biomass in a fire-regenerated scrub-oak ecosystem. Global Change Biology 8:90–103.

Dilustro, J. J., F. P. Day, B. G. Drake, and C. R. Hinkle. 2002. Abundance, production and mortality of fine roots under elevated atmospheric carbon dioxide in an oak-scrub ecosystem. Environmental and Experimental Botany 48: 149–159.

Doolittle, J. A., F. E. Minzenmayer, S. W. Waltman, and E. C. Benham. 2002. Ground penetrating radar soil suitability map of the conterminous United States. Pages 7–12 *in* S. Koppenjan and H. Lee, editors. Ninth International Conference on Ground Penetrating Radar (Santa Barbara, California, USA, 29 April–2 May 2002). Proceedings of SPIE, International Society of Optical Engineering, Bellingham, Washington, USA.

Drake, B. G., P. W. Lendley, W. J. Arp, D. Nassiry, and P. S. Curtis. 1989. An open top chamber for field studies of elevated atmospheric $CO_2$ concentration on salt marsh vegetation. Functional Ecology 3:363–371.

Fitter, A. H. 1987. An architectural approach to the comparative ecology of plant root systems. New Phytologist 106:61–77.

Fitter, A. H., and T. R. Stickland. 1992. Architectural analysis of plant root systems III: studies on plants under field conditions. New Phytologist 121:243–248.

Fogel, R. 1985. Roots as primary producers in belowground ecosystems. Pages 23–36 *in* A. G. Fitter, D. Atkinson, D. J. Read, and M. B. Usher, editors. Interactions in soil. Special

Publication of the British Ecological Society Number 4. Blackwell, Oxford, UK.
GSSI [Geophysical Survey Systems Incorporated]. 2004. Radan 6.0 user's manual. GSSI, North Salem, New Hampshire, USA.
Hendrick, R. L., and K. S. Pregitzer. 1992. The demography of fine roots in a northern hardwood forest. Ecology 73: 1094–1104.
Hruska, J., J. Cermak, and S. Sustek. 1999. Mapping tree root systems with ground-penetrating radar. Tree Physiology 19: 125–130.
Huckle, H. F., H. D. Dollar, and R. F. Pendleton. 1974. Soil survey of Brevard County, Florida. USDA Soil Conservation Service, Washington, D.C., USA.
IPCC [Intergovernmental Panel on Climate Change]. 2001. Climate change 2001: the scientific basis. J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. Van der Linden, X. Dai, K. Maskell, and C. A. Johnson, editors. Contributions of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411.
Johnston, C. A., et al. 2004. Carbon cycling in soil. Frontiers in Ecology and the Environment 2:522–528.
Korner, C. 2001. Biosphere responses to $CO_2$ enrichment. Ecological Applications 10:1590–1619.
Korner, C., and J. A. Arnone. 1992. Responses to elevated carbon dioxide in artificial tropical ecosystems. Science 257: 1672–1675.
Leckebusch, J. 2003. Ground-penetrating radar: a modern three-dimensional prospection method. Archaeological Prospection 10:213–240.
Mailander, J. L. 1990. Climate of Kennedy Space Center and vicinity. NASA Technical Memorandum 103498. Kennedy Space Center, Florida, USA.
Miller, A. T., H. L. Allen, and C. A. Maier. 2006. Quantifying the coarse-root biomass of intensively managed loblolly pine plantations. Canadian Journal of Forest Research 36:12–22.
Mooney, H. A. 1991. Biological response to climate change: an agenda for research. Ecological Applications 1:112–117.
Mooney, H. A., B. G. Drake, R. J. Luxmoore, W. C. Oechel, and L. F. Pitelka. 1991. Predicting ecosystem responses to elevated $CO_2$ concentrations. BioScience 41:96–104.
Nielsen, K. J., J. P. Lynch, and H. N. Weiss. 1997. Fractal geometry of bean root systems: correlations between spatial and fractal dimension. American Journal of Botany 84: 26–33.
Norby, R. J. 1994. Issues and perspectives for investigating root responses to elevated atmospheric carbon dioxide. Plant and Soil 165:9–20.
Norby, R. J., and R. B. Jackson. 2000. Root dynamics and global change: seeking an ecosystem perspective. New Phytologist 147:3–12.
Norby, R. J., E. G. O'Neill, S. D. Wullscleger, C. A. Gunderson, and C. T. Nietch. 1993. Growth enhancement of *Quercus alba* saplings by $CO_2$ enrichment under field conditions. Bulletin of the Ecological Society of America 74: 375.
Oppenheim, A. V., and R. W. Schafer. 1975. Digital signal processing. Prentice Hall, Englewood Cliffs, New Jersey, USA.
Pierret, A., C. J. Moran, and C. Doussan. 2005. Conventional detection methodology is limiting our ability to understand the roles and functions of fine roots. New Phytologist 166: 967–980.
Poorter, H., and M. L. Navas. 2003. Plant growth and competition at elevated $CO_2$: on winners, losers and functional groups. New Phytologist 157:175–198.
Pregitzer, K. S., D. R. Zak, P. S. Curtis, M. E. Kubiske, J. A. Terri, and C. S. Vogel. 1995. Atmospheric $CO_2$, soil nitrogen and turnover of fine roots. New Phytologist 129:579–585.
Robinson, D., A. Hodge, and A. Fitter. 2003. Constraints on the form and function of root systems. Pages 1–32 *in* H. de Kroon and E. J. W. Visser, editors. Root ecology. Springer, New York, New York, USA.
SAS Institute. 1990. MIXED procedure. SAS Institute, Cary, North Carolina, USA.
Schlesinger, W. H. 1991. Biogeochemistry: an analysis of global change. Academic Press, New York, New York, USA.
Schmalzer, P. A., and C. R. Hinkle. 1987. Effects of fire on composition, biomass and nutrients in oak scrub vegetation on John F. Kennedy Space Center, Florida. NASA Technical Memorandum 100305. Kennedy Space Center, Florida, USA.
Schmalzer, P. A., and C. R. Hinkle. 1991. Dynamics of vegetation and soils of oak/saw palmetto scrub after fire: observations from permanent transects. NASA Technical Memorandum 103817. Kennedy Space Center, Florida, USA.
Schmalzer, P. A., and C. R. Hinkle. 1992. Recovery of oak–saw palmetto scrub after fire. Castanea 57:158–173.
Systat. 2004. SigmaScan Pro 5.0. Systat Software, Point Richmond, California, USA.
Waisel, Y., A. Eshel, and U. Kafkafi. 2002. Plant roots: the hidden half. Marcel Deckker, New York, New York, USA.
Ward, J. K., and B. R. Strain. 1999. Elevated $CO_2$ studies: past, present and future. Tree Physiology 19:211–220.
Wielopolski, L., G. Hendey, and M. McGuigan. 2000. Imaging tree root systems in situ. Pages 642–646 *in* D. A. Noon, G. F. Stickley, and D. Longstaff, editors. Eighth International Conference on Ground-Penetrating Radar (Gold Coast, Queensland, Australia, 23–26 May 2000). Volume 4084. Proceedings of SPIE, International Society of Optical Engineering, Bellingham, Washington, USA.