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Differential aluminum and calcium concentratins in the tissues of ten Cornus species

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RICHARDSON, A. D., E. G. DENNY, J. A. FORBUSH, T. G. SICCAMA, AND K. S. HUNTER (Yale University, School of Forestry and Environmental Studies, 370 Prospect St., New Haven, CT 06511). Differential aluminum and calcium concentrations in the tissues of ten Corpus species. J. Torrey Bot. Soc. 128: 000-000. 2001.-In both ornamental and forested environments, dogwood anthracnose has caused widespread dieback and decline of Corpus florida L., flowering dogwood, since the late 1970s. Early observations of this disease were more or less simultaneous with the peak of acid rain in North America. Aluminum is known to be toxic to some plants at low concentrations, and soil availability of Al, and hence plant uptake, may be increased by acid rain. Experimental treatment with simulated acid precipitation has been shown to increase the severity of anthracnose infection. In a preliminary study, we observed surprisingly high levels of At in C. florida wood. Suspecting a possible link between At and anthracnose, we hypothesized that At concentrations would be higher in anthracnose-susceptible Corpus species. We also hypothesized that anthracnose-infected C. florida would have higher levels of foliar Al than uninfected trees. Finally, we hypothesized that if there was indeed a link between acid rain and anthracnose via At uptake and toxicity, that younger wood should have higher concentrations of Al than older wood, reflecting increased soil availability of Al. To investigate the first hypothesis, we collected tissue samples from ten Corpus species from locations across North America for chemical analysis. The four large-bracted species, C. florida, C. nuttallii And., C. kousa (Buerger ex Miq.) Hance and C. canadensis L., accumulated At at concentrations an order of magnitude greater than any of the small-bracted species we studied. However, C. florida and C. nuttallii are known to be highly susceptible to infection by dogwood anthracnose, while C. kousa and C. canadensis are considered resistant to infection. To investigate the second hypothesis, we collected leaves from infected and uninfected trees growing on the same site; Al concentrations in leaves from uninfected trees were actually 432 ppm higher than those from infected trees, suggesting that At toxicity is not likely a factor in the severity of anthracnose infection. To investigate the third hypothesis, we examined tissue chemistry of both old and young wood. We found that At concentrations in C. florida wood decreased from older wood to younger wood, contrary to what we would expect if At availability (and hence plant uptake) had increased as a consequence of acid rain.

Key words: acid precipitation, Al: Ca ratio, aluminum, calcium, Cornus, dogwood anthracnose, plant tissue' chemistry.

The dogwood genus, Corpus, comprises some 45 species, most of which are native to North America, Europe and Asia (Hudak 1984). The genus includes herbs (e.g. Corpus canadensis L., bunchberry), shrubs (e.g. C. amomum Mill., silky dogwood), and trees (e.g. C. florida L., flowering dogwood) (nomenclature follows Gleason and Cronquist 1991). Corpus florida is an exceptionally popular ornamental tree, used in landscape settings throughout most of the eastern United States. It is also an important native understory tree from Maine west to Iowa, and south to Florida and Texas. The health of C. florida in southeastern New York and southwestern Connecticut was observed to decline beginning in 1978. It was subsequently demonstrated that a fungus in the genus Discula Sacc. was the causal agent of the disease known as dogwood anthracnose. This disease has since caused widespread mortality of C. florida across most of its range. Because of the economic and ecological importance of flowering dogwood, dogwood anthracnose continues to be the subject of numerous studies (e.g. Hiers and Evans 1997; Schwegman et al. 1998; Britton et al. 1998; Williams and Moriarty 1999).

In a previous unpublished study, we noticed a high concentration of Al in a single analyzed sample of C. florida wood. We wondered whether high levels of this toxic element might in some way be related to recent dogwood declines. Aluminum uptake has been linked to decline of sugar maple (Acer saccharum Marsh.) in Ontario, Canada (Mohamed et al. 1997) and red spruce (Picea rubens Sarg.) in the southeastern United States (Joslin et al. 1992). Onset of dieback and decline of flowering

dogwood occurred more or less concurrently with the peak of acid rain in the late 1970s. Although these two events may be unconnected, acid deposition is known to alter the availability of certain cations, including Al and Ca, on the soil exchange complex (Reuss and Johnson 1986). In a number of cases, acid deposition has been linked both directly and indirectly to forest tree diseases (reviewed by Britton et al. 1998). Dogwood anthracnose has spread to areas outside the range normally associated with severe acid rain (e.g., the southern Appalachians and the Pacific Northwest), but a connection between acid rain and severity of dogwood anthracnose infection has been experimentally demonstrated (Britton et al. 1996, 1998). The mechanism involved is not clear; one possibility may be that acid precipitation-altered soil chemistry has resulted in increased plant uptake of Al, since Al uptake is known to be directly related to soil availability (Jansen et al. 2000). If plant tissue concentrations of Al reached toxic levels, we thought it possible that these trees could be weakened and thus predisposed to anthracnose infection. Reversing this line of reasoning, we hypothesized that Al concentrations would be higher in anthracnose-susceptible species, although we recognized that there are differences among species with regard to toxicity thresholds (Kochian 1995). We further hypothesized that more heavily infected C. florida trees would have higher Al concentrations than less heavily infected (or uninfected) C. florida trees growing at the same site. Finally, we hypothesized that, if acid rain had indeed altered soil Al availability, older C. florida wood would have lower Al concentrations than younger, or more recently laid-down, C. florida wood.

To investigate our hypotheses, we examined Al and Ca concentrations in a variety of anthracnose-susceptible and non-susceptible dogwood species and some associated shrubs on the same sites. We also examined foliar Al and Ca concentrations in heavily infected and uninfected C. florida trees, and we compared Al concentrations in annual rings of different years. We recognized that our approach would not be a direct test of the link between Al and anthracnose, but anticipated that the results could provide the justification for further experimental work.

Methods. To investigate differences among dogwood species, leaf and branchlet samples (representing 2-3 years of growth) were collected from ten Corpus species growing in different locations across North America. Where possible, sites featuring two or more Corpus species growing in close proximity were selected. Since this project was started in the early winter of 1998, the initial collections of branchlets occurred after leaf fall. Leaf and some additional branchlet samples were also collected during the following spring and summer.

We obtained samples from the following commonly occurring species: C. florida (7 sites), C. amomum (4 sites), C. sericea L. (red-osier dogwood, 3 sites), C. alternifolia L.f. (alternate-leaf dogwood, 4 sites), C. racemosa Lam. (gray dogwood, 3 sites), C. canadensis (3 sites), C. nuttallii Aud. (Pacific dogwood, 2 sites), C. kousa (Buerger ex Miq.) Hance (Japanese dogwood, 2 sites), C. rugosa Lam. (roundleaf dogwood, 1 site), and C. mas L. (cornelian cherry, 1 site). Samples of some common associated shrubs, such as Rosa multiflora Thunb. (multiflora rose), Acer spicatum Lam. (mountain maple), and Rhus typhina L. (staghorn sumac), were collected for comparison. All samples were collected in natural woodlands and edges, with the exception of C. florida, C. mas and C. kousa samples collected from ornamental trees at Yale University, New Haven, CT, and urban C. nuttallii collected from a park in Seattle, WA.

Four or five branchlets were collected from each of four or five individuals to produce a composite sample for each site. Samples were put into clean paper bags. In the laboratory we separated branchlets and leaves and then ovendried samples at 80 deg C to a constant weight. Dry samples were ground in a Wiley Mill. Mixed, oven-dry subsamples (0.3 g) were ashed and the resulting ash was dissolved in 8 ml 6N nitric acid, filtered, and diluted with distilled deionized water to 50 ml. Solutions were analyzed for Al, Ca, Cu, Fe, K, Mn, Mg, P, Pb and Zn on a Perkin Elmer Optima 3000 Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP-AES). Beginning at the dry ashing stage, blanks and a standard reference material (apple leaves) were processed simultaneously with all tissue samples to maintain quality control.

To investigate a possible relationship between the severity of anthracnose infection and tissue Al concentrations, we collected samples from five sites in the vicinity of New Haven, CT. At each site, we identified two C. florida trees, one of which we judged

to be heavily infected with dogwood anthracnose, and one of which we judged to be either uninfected or much less severely infected. We collected leaves from each tree and then processed them for ICP-AES analysis as described above. A two-tailed t-test, with trees paired by site, was used to test for differences in tissue chemistry between infected and uninfected trees.

To compare tissue chemistry of C. florida wood with that of other important New England hardwoods, we analyzed samples from more than a dozen common tree species. Samples came from one site in New Hampshire and two sites in Connecticut, and were collected over the last 15 years. Breast height cores were taken with an increment borer, oven dried, and then processed according to the digest and analysis procedures described above. Only light wood was included in these samples; the chemistry of dark heartwood or disease-stained wood is known to be quite different from light wood (Likens and Bormann 1970). Reported values are the arithmetic mean of results from two or more trees.

To compare tissue chemistry of old and young C. florida wood, wood and bark samples were obtained from the lower boles of four harvested C. florida trees (six for bark) from southern Connecticut. Wood of different ages was sampled by drilling vertically into bole cross-sections at four well-spaced radial points. Annual rings of polished cross-sections were counted under a dissection microscope in order to determine the years included in each drilled wood sample. Bark was peeled off the bole and ground in a Wiley Mill. Wood and bark were ovendried, dry ashed, dissolved in nitric acid, and analyzed as described above.

Results. Aluminum concentrations in the branchlets of three species (C. kousa, C. florida and C. nuttallii) were about 20 times higher than in any of the other Comus species we examined (Table 1). The mean Al concentration across these three species was 600 ppm. Furthermore, compared to some associated shrubs (e.g. A. spicatum, 14 ppm; R. typhina, 26 ppm; R. multiflora, 33 ppm), these values are noticeably high. These same three Corpus species, as well as C. canadensis, also had relatively high (mean 800 ppm) foliar Al concentrations. All Corpus branchlet samples appeared to have similar Ca concentrations (ca. 1.0-1.5%), but these values were not much higher than those of the associated shrubs we tested (e.g. R. typhina branchlets, 0.7%; R. multiflora and A. spicatum branchlets, 1.3%). Foliar Ca concentrations for all Cornus species were about 2-3% for most species. Figure I illustrates the AI:Ca ratio in branchlets and/or leaves for the species studied. Even relative to their Ca content, C. kousa, C. florida, C. nuttallii, and C. canadensis demonstrated higher Al concentrations in their leaves and branchlets than other species. There were no appreciable species-related differences in concentrations of other elements (Cu, Fe, K, Mn, Mg, P Pb and Zn).

Aluminum concentrations in the leaves of heavily infected C. florida trees averaged 931 ppm; in uninfected trees the figure was 1363 ppm (Table 2). At all five sites, Al concentrations in the uninfected trees were consistently higher than in the infected trees (difference of 432 +/- 48 ppm, mean +/- 1 SE). A paired t-test indicated that this difference was significant at P

Compared to Al concentrations in the wood and bark of other New England tree species (Table 3), C. florida ranks among the highest species in wood Al concentration. Bark Al concentration in C. florida (over 1600 ppm) was more than five times greater than in any other species we have studied, and a hundred times greater than in several species. Furthermore, we observed that Al concentrations showed a decreasing trend from older to younger wood within the four individual mature stems we studied. In wood laid down during the last 10 years, the Al concentration averaged 47 ppm. Twenty year old wood had a mean Al concentration of 57 ppm, but 50 year old wood (129 ppm) and 60+ year old wood (188 ppm) had dramatically higher Al concentrations. The positive correlation between wood age and aluminum concentration (R == 0.719) was significant at P

Discussion. Our study of the Al and Ca concentrations in the branchlets and leaves of different Comus species was motivated by the current interest in dogwood anthracnose, and what we thought might be a link between this disease and plant tissue chemistry. Aluminum is not known to be an essential plant nutrient and is toxic to some plants at certain levels (Rengel 1992; Kochian 1995). We suspected that high levels of this element in their tissues might predispose some Corpus species to anthracnose, and hypothesized higher Al levels in anthracnose-susceptible Corpus species, and higher Al levels in infected C. florida than in uninfected C. florida. However, these hypotheses were not validated by our results. Of the four species

exhibiting high Al concentrations in their tissues, only two, C. florida and C. nuttallii, are highly susceptible to infection. Corpus kousa is generally considered to be a host but displays little evidence of pathogenic foliar infection, except under continuously wet conditions; some cultivars of C. kousa appear less resistant to infection than others (Daughtrey and Hibben 1994; Daughtrey et al. 1996). Corpus canadensis does not seem to be susceptible at all (Hibben et al. 1991). Other native and ornamental Corpus species, including those which we found to have low Al concentrations, are generally considered resistant to anthracnose infection (Daughtrey et al. 1996). Individual C. florida seedlings which may be resistant to infection have been identified, but the cause of this resistance, and the resistance of other Cornus species, is unknown (Britton et al. 1996). This is one reason why there has been little success to date in developing disease-resistant C. florida, either through targeted breeding programs or genetic engineering (Britton et al. 1996).

Certain plant species are Al accumulators (Chenery 1948; Chenery and Sporne 1976; Vogt et al. 1987; Jansen et al. 2000). It is not known whether Al accumulation benefits or stresses these species, although Al accumulation is thought to enable some species to tolerate the high-Al soils of the wet tropics. Accumulators are defined by Chenery and Sporne (1976) to be plants with more than 1000 VLg Al/g oven-dry plant weight (1000 ppm). By this definition, our results suggest that both C. florida and C. kousa have the potential to qualify as aluminum accumulators. An early study (Chenery 1948) actually suggested that certain Corpus species might be Al accumulators, although the accuracy of the methods used has been more recently called into question (Eyde 1988). We would like to point out that those Corpus species which we found to be highest in Al are also those with large flower bracts. The Corpus species with comparatively low Al concentrations all have small flower bracts. Bract size has long been considered to be of evolutionary significance in this genus (Johnson 1931). Eyde (1988) suggested that the large bracts evolved to attract insect pollinators, and Murrell (1993) claimed that these showy structures actually evolved twice in the genus, implying convergent evolution. The systematics of Corpus are complex, and there is much disagreement in the literature on the evolution of the genus (Eyde 1988; Murrell 1993; Hardin and Murrell 1997; Xiang et al. 1996). In Eyde's (1988) scheme, there are two dogwood lineages: the red fruit species, and the blue/white fruit species; the red fruit species can then be subdivided into the cornelian cherries and the large-bracted dogwoods (the large-bracted group includes some Asian species in addition to the four species we studied). More recent work (Xiang et al. 1996) based on sequence data from chloroplast DNA generally agrees with Eyde's morphological classification. Aluminum accumulation is regarded by Chenery and Sporne (1976) as a trait well-correlated with various primitive characters, but Eyde (1988) argues from many angles that the large-bracted dogwoods are advanced, not primitive, and that it is the blue/white fruit species which must be considered ancestral. Therefore, although Al accumulation is correlated with primitive traits in other genera, high Al seems to be a trait of some of the more advanced species in the dogwood genus.

Calcium can ameliorate some of the toxic effects of Al (Rengel 1992). For this reason the Al: Ca ratio has been suggested (Rengel 1992) as a better measure of potential Al toxicity in plants than the absolute Al concentration. The leaf tissues of most of the large-bracted Cornus species we analyzed contained well over 2% calcium by weight. In fact, C. florida has been referred to as a "calcium pump" because its leaf litter contains such high concentrations of Ca (Thomas 1969; Vimmerstedt 1965). However, some of the small-bracted Comus species have similarly high levels of foliar Ca. Although Ca may act as an agent to mediate aluminum toxicity, it does not appear that the large-bracted Cornus species we studied accumulated extra calcium to offset the potentially toxic effects of high Al. Rather, the large-bracted species all had similarly high Al: Ca ratios, which were more than three times as high as the ratios for the small-bracted Comus species.

Site factors (such as light, rainfall, temperature, aspect, elevation, geographic features and stem density) are known to account for some of the variability in the severity of anthracnose infection of C. florida (Daughtrey and Hibben 1994; Chellemi et al. 1992). However, differences in Al concentrations among species cannot be attributed merely to differences in soil conditions and nutrient availability, as they persisted even on sites where we sampled multiple Cornus species (i.e. Bethany, Guilford, Wallingford, Longford Township and Mt. Baker National Forest). For example, the foliar Al concentration at our Bethany drumlin site (a former pasture) ranged from 1428 ppm in C. florida to 24 ppm in C. amomum and 36 ppm in C. racemosa, although all were growing on similar soils. Such differences indicate that our results are related more to species-specific

differences in uptake than site-specific soil characteristics. There may be seasonal variation in Al and Ca tissue chemistry, but there is no clear annual pattern apparent in our results, and in C. florida, both leaf and branch concentrations of Al were comparatively high (> 300 ppm) regardless of the month of collection. We acknowledge, however, the considerable range in concentrations present within the species studied: for example, Al in C. florida leaves collected from Guilford, CT in September (1596 ppm) was more than four times greater than Al in C. florida leaves collected from the Shenandoah Mts., VA, in May (341 ppm). This range may be due in part to confounding effects of time of collection, site characteristics, and intra-population variability in Al uptake.

To our great surprise, the C. florida trees which we judged to be most heavily infected with dogwood anthracnose had lower foliar Al concentrations than those trees which were either uninfected or less severely infected. This result was precisely the reverse of our second hypothesis, and appears to refute the idea that Al toxicity weakens C. florida trees and makes them more susceptible to infection with anthracnose. If anything, the results could be interpreted as indicating that high levels of Al confer some benefit to the tree, and make it a less suitable host for the Discula destructiva fungus that is the cause of dogwood anthracnose. This speculation needs to be investigated further and tested experimentally.

Annual trends in bolewood Al concentration are noteworthy because other studies have found the opposite trend in other species, and it has been suggested that element concentrations in wood of different ages can be used as indicators of changes in atmospheric deposition or other anthropogenic stressors (Matusiewicz and Barnes 1985; Berish and Ragsdale 1985; Bondietti et al. 1989; Zayed et al. 1991; Dion et al. 1993). Our data show lower Al concentrations in more recently formed wood, whereas other studies show higher Al concentrations in more recently formed wood. Nutrient concentrations in wood are considered indicative of the soil nutrient availability at the time the wood was laid down. Thus the trends we observed appear to contradict hypothesized increases in soil availability of Al related to acid rain. Our results seem to suggest that Al availability in the soil may have decreased over the last 50 years, although we know of no studies that have documented such a change. A possible alternative explanation, which needs to be tested, is that as an adaptation to C. florida's propensity for Al accumulation, Al is continually re-translocated away from sapwood and phloem to non-functional heartwood and cork tissue (reported for Ca in Chamaecyparis thyoides (L.) B.S.P., Atlantic white-cedar, by Andrews and Siccama 1995). If this were the case, then more recently formed wood could have lower concentrations of Al, even if soil availability of Al was increasing over time.

Prior to conducting this research, we had hypothesized that At concentrations would be higher in anthracnose-susceptible Corpus species than in non-susceptible species. The trends in tissue chemistry did not support this hypothesis, since some non-susceptible Cornus species were found to have high concentrations of At in their tissues. However, we did document an interesting pattern of Al accumulation which indicates physiological differences between the large- and small-bracted Corpus species of diverse growth habit (both woody trees and an herbaceous shrub). Furthermore, we found that, contrary to our second hypothesis, higher levels of foliar At were associated with less severe infection by dogwood anthracnose. This result suggests that Al toxicity is not predisposing C. florida to infection. Finally, annual trends in bolewood At deposition for C. florida are the reverse of what has been reported in the literature for other species, which brings into question our hypothesized acid rain link. Together, these results do not support the suggested connection between acid rain, Al toxicity, and dogwood anthracnose, but they do suggest some interesting avenues for future research into At accumulation in the dogwoods. Of greatest interest in this regard is our observation that uninfected C. florida leaves had much higher concentrations of At than infected leaves.

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Received for publication October 14, 2000, and in revised form February 5, 2001.

1 Laboratory analysis for this project was made pos- sible by a grant from the Leonard G. Carpenter Fund, School of Forestry and Environmental Studies, Yale University, and the Quinnipiac River Foundation, New Haven, CT We thank C. E. Williams for helpful comments on an early version of this paper.

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