

THE DEVELOPMENTAL STREAM OF COTTONWOODS AFFECTS RAMET GROWTH AND RESISTANCE TO GALLING APHIDS

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Abstract. We define the “developmental stream” of a plant as the gradient of increasingly mature phenotypes its shoots express over its lifetime. This pattern has important implications for studies of morphology, physiology, reproduction, and interactions with other organisms. Using cottonwoods, we test two major hypotheses about their developmental streams. First, within a tree, the developmental stage expressed by a shoot is dependent on its growth distance from the ground. Second, the distribution and fitness of *Pemphigus betae*, an aphid that is sensitive to host maturity, are positively related to increasingly mature shoot phenotypes within a tree. We show that the developmental variation in plant morphology and reproductive output within a tree are as great as that found among different-aged trees within a clone. In addition, we show that within-tree patterns of variation are stable from year to year and that *P. betae* responds to this variation by preferentially colonizing branches expressing more mature phenotypes. This pattern of branch selection is adaptive; aphids transferred to branches with shoots expressing mature phenotypes have expected fitnesses >80% higher than those transferred to branches expressing juvenile phenotypes.

These findings have several general implications. First, a within-tree series of developmental stages provides a heritable mechanism for creating mosaics of variability in host quality within plants that create host selection problems for herbivores. Second, herbivores sensitive to developmental changes in their hosts will be concentrated in areas of high quality where they will be subject to the detrimental effects of competition, predation, and parasitism. Third, simulation models of plant growth based on the behavior of repeating plant parts (e.g., shoots) must be sensitive to developmental changes in these parts during plant development. Fourth, the developmental streams of plants may affect the evolution of such herbivore traits as territoriality, deme formation, and virulence. Fifth, the use of clonally propagated stock for the study of the genetic components of resistance to herbivory must be carried out with an understanding of the effects of host development on herbivores.

Key words: aphid; cottonwood; gall; heterochronic evolution; herbivory; host development; metamerism; mosaicism; Pemphigus; phase change; Populus; resistance.

INTRODUCTION

The processes of growth and development differ between plants and animals in profound and important ways. Rather than growing by an increase in the size of a small number of distinct organs, growth in long-lived plant species results from the proliferation of modules (here: current-year shoots). In animal development, individual organs mature and senesce, while long-lived plants produce new modules in successive growing seasons whose behavior changes over time (maturation or phase change). For example, a *Eucalyptus* ramet, whose shoots grow vigorously and produce juvenile leaves (connate vs. petiolate, opposite and entire vs. alternate and dissected) and no flowers, is considered juvenile (Cameron 1970, Bennett et al. 1986, Wiltshire et al. 1991). If at least some shoots bear mature-form leaves and/or flowers and grow more slowly, the entire ramet is considered mature.

Manuscript received 10 June 1996; revised 2 December 1996; accepted 24 January 1997; final version received 11 February 1997.

Developmental processes in plants (ordered, directional changes in shoot behavior) have many causes, most of which are generalizable into two broad categories: ontogenetic and physiological mechanisms (Brink 1962, Fortanier and Jonkers 1976, Hood and Libby 1978, Huchison et al. 1990, Poethig 1990, Lawson and Poethig 1995). Ontogenetic changes arise from modification of gene activity in the meristems; genes are turned on or off, or their activity is altered (Longman and Wareing 1959, Brink 1962, Zagory and Libby 1985, Huchison et al. 1990, Poethig 1990) in ways that cause phenotypic changes in the organs subsequently produced by the meristems. Physiological processes result from alterations in the environment of the meristems; hormone levels, shoot–root imbalances, water and nutrient relations, shading, and herbivore damage can create altered physiological environments of meristems, which cause alteration of shoot behavior (Brink 1962, Fortanier and Jonkers 1976, Foggo et al. 1994).

We term the gradient of increasingly mature shoot phenotypes the “developmental stream” after Lillie

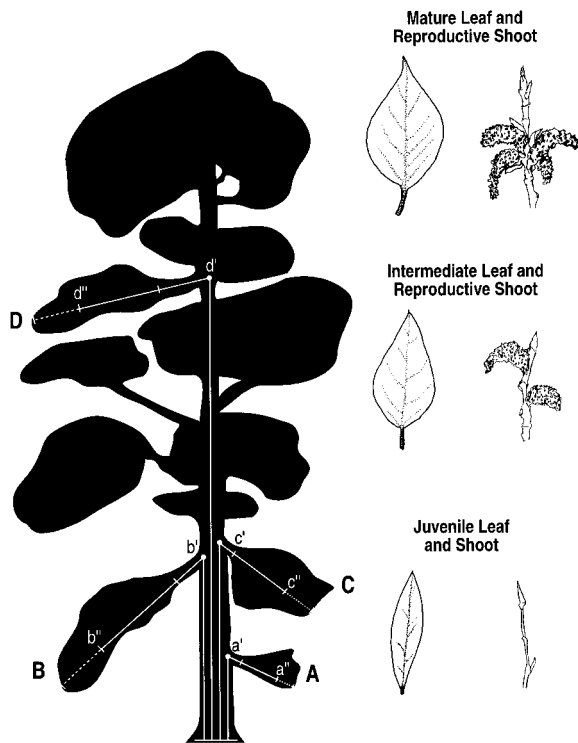


FIG. 1. Calculation of developmental distance. For branch A in this example, developmental distance is measured as the sum of the distances from the root crown to the point of branch insertion (a'), to the first vegetative shoot, and from the first vegetative shoot to two-thirds the distance the branch apex (a''). Distances for shoots on branches A, B, and D are obviously different; less obvious are branch growth differences between branches such as B and C. Leaves and shoots characteristic of juvenile, intermediate, and mature sections of a mature tree are illustrated on the right of the figure.

(1927) who challenged his colleagues to “explain how an unchanging [gene] complex can direct the course of an ordered developmental stream” (p. 367). By this we can include all facets of shoot behavior, measurable in morphology, physiology, reproduction, and resistance characters. This does *not* imply that characters are under direct transcriptional control. In this paper, we do not differentiate among sources of phenotypic variation, but use the term development to denote age-related changes in ramet characters.

The developmental stream produces a seemingly paradoxical pattern of within-plant variation in which shoots in the chronologically oldest (i.e., more basal) regions will express the developmentally youngest phenotypes (Fig. 1; Fortanier and Jonkers 1976, Greenwood 1984, Zagory and Libby 1985, Poethig 1990). Both ontogenetic and physiological processes work in ways that cause modules farther from the root crown to express more mature phenotypes (Soegaard 1956, Libby et al. 1972, Libby and Hood 1976, Steele et al. 1989, Greenwood and Hutchinson 1993). Ontogenetic mechanisms, such as cell cycle “clocks” (Holliday and

Pugh 1975, Caplan and Ordahl 1978, Greenwood 1984, Zagory and Libby 1985), predict that shoots at greater growth distances from the root crown (and hence at a larger number of divisions by meristematic cells in annual cycles of shoot extension) will express an increased degree of maturity (Holliday and Pugh 1975, Hood and Libby 1978, Greenwood et al. 1989, Poethig 1990). Physiological mechanisms, produced by hormonal gradients (Khait 1986) or hydraulic architecture and overly complex vascular connections (Zimmermann 1982, Joyce and Steiner 1995), predict that shoot phenotypes will change according to their separation from the root crown (Robbins 1957, Fortanier and Jonkers 1976, Poethig 1990, Haffner et al. 1991). In either case, the distance from the root crown to a shoot should be a good predictor of a shoot’s position in the developmental stream (Schaffalitzky de Muckadell 1954, 1956), and the arrangement of modules in space defines the degree of development of the plant as a whole. Thus, a developmental stream leads to a “distance hypothesis” (Poethig 1990) in which traits vary with their degree of separation from the root crown.

Plant ecologists recognize many levels (Suomela and Ayres 1994, Suomela and Nilson 1994) and sources of variation in host quality within plants in the suitability of modules for herbivores. Competition for nutrients, photosynthates and sunlight among modules (Borchert and Slade 1981, Remphry and Powell 1982, Jones 1985), herbivore-induced variation (Green and Ryan 1972, Bryant 1981, Bryant et al. 1983, Tallamy 1985, Craig et al. 1986, Roininen et al. 1988, Karban and Niiho 1995) and somatic mutation (Whitham and Slobodchikoff 1981), can all affect host quality within individuals.

Developmentally based variation in host quality, on the other hand, has been much less emphasized by ecologists until recently (Price et al. 1987a, b, Kearsley and Whitham 1989, Price 1989), despite centuries of well-documented cases in the horticultural and botanical literature (Brink 1962, Poethig 1990, Lawson and Poethig 1995, and references therein). This may be due to a lack of interdisciplinary communication, or perhaps the difficulty in defining an “individual” in plants in a way that is both ecologically and statistically satisfying (Soegaard 1956, Jones 1985, Zagory and Libby 1985, Kearsley and Whitham 1989).

In this study we quantified the developmental stream of cottonwoods by examining four major questions arising from the distance hypothesis. First, within individual ramets, are there predictable changes in plant morphological traits that correlate with the distance of a shoot from the root crown? Second, how do these measures of distance-based phase changes relate to the distribution of the galling aphid *Pemphigus betae*? Third, having demonstrated a strong association of aphids and the mature branches of trees, we then examined the adaptive nature of this distribution by quantifying the fitness of aphids that were experimentally

transferred to branches exhibiting different phase states within ramets. Fourth, how does the within-ramet variation in morphology and aphid performance compare to the variation arising among ramets from different clones in the population? Our results showed that the developmental stream produces predictable within-ramet variation in morphology and host quality that can be nearly equal to that seen among ramets of different clones.

METHODS

Natural history of Pemphigus betae and Populus angustifolia

Pemphigus betae is a leaf-galling aphid with a complex life cycle (Moran and Whitham 1988). In early April, fundatrices, members of a wingless parthenogenetic life stage, emerge from overwintering eggs, crawl out on branches, and initiate gall formation along the midvein of expanding leaves. Unsuccessful stem mothers die within 3 d of attempting gall formation and leave a characteristic scar at the site of the attempt (Whitham 1978). Only first-flush leaves, those whose primordia were formed in the previous season, are available to stem mothers. Successful fundatrices produce a mature gall and 10–300 offspring, which migrate in July to secondary hosts.

Narrowleaf cottonwood, *Populus angustifolia* and its naturally occurring backcrosses with Fremont cottonwood (*Populus fremontii*) grow in floodplains of rivers in the southwestern United States (Eckenwalder 1984, Whitham 1989). Ramets sucker from extensive shallow root systems, forming clones (Kearsley and Whitham 1989). As shoot elongation proceeds during the growing season, buds are laid down in the leaf axils; vegetative buds occupy terminal and subterminal positions. Flowers, when present, occupy more basal positions. We define “shoot” as the current year’s vegetative growth, “ramet” or “tree” as the individual tree within a clone, and “clone” for the collection of all ramets derived from a single seed. Although cottonwoods are heterophyllous, producing morphologically distinct early- and late-flush leaves, this paper deals only with the first-flush leaves, because only these leaves are used by *P. betae* (Whitham 1978, Kearsley and Whitham 1989). Previous studies (Kearsley and Whitham 1989 and unpublished data) have shown that among juvenile and mature ramets of a clone, mature ramets have larger, broader leaves with longer petioles, abbreviated leaf flushes, a greater number of flowers per shoot, and a gradual increase in susceptibility to attack by *Pemphigus betae*. Here we focus on a finer within-ramet level of development and compare developmental variation in traits within ramets with variation among ramets.

Tree development and developmental distance

In order to sample development within individual ramets we needed some measure of a shoot’s separation

from the root crown. We used “developmental distance,” a simple linear distance measure, because it would affect hormone gradients, water relations, meristematic cell divisions, and intercellular communication distance, any of which may affect the phenotypes of shoots (Fortanier and Jonkers 1976, Kramer and Kozlowski 1979, Roulund 1979, Greenwood 1984, Clancy and Price 1986, Khait 1986, Price and Clancy 1986). Fig. 1 shows graphically how this distance was calculated. For example, for shoots on branch A, the developmental distance is the sum of the distances from the root crown to the point of branch insertion (a'), from the center of the trunk to the first vegetative shoot, and two thirds the distance from the first shoot to the tip of the branch (a''). By using the latter two distances we produced a measure of the average growth distance for shoots on a branch, given the clustering of shoots towards the distal end of the branch. Note that branches with similar insertion heights (i.e., B and the branch inserting opposite) can have very different developmental distances.

Morphological correlates of development

We measured four morphological correlates of development (Kearsley and Whitham 1989, and unpublished data) in branches from 12 mature ramets in separate, naturally occurring clones along the Weber River, ~17 km south of Ogden, Weber County, Utah, USA. Trees were selected based on two criteria: (1) some degree of flowering and (2) branches distributed throughout the length of the trunk. Within each tree, we selected 10 major branches for study and climbed each tree to measure developmental distances manually.

To assess the degree of within-ramet developmental variation in shoot morphology we first measured three leaf characters. Two of these were leaf shape characters: relative blade width (width/length) and relative petiole length (petiole length/blade length). We measured blade width, blade length, and petiole length from the middle first-flush leaf on 20 haphazardly selected terminal shoots from each branch. We calculated mean leaf area from these shoots by measuring the average dry mass per leaf, an accurate predictor of leaf area, for each shoot (Kearsley and Whitham 1989). All undamaged leaves from each shoot were counted, dried, and weighed. Shoot means for all three characters were averaged within branches.

We used the ratio of reproductive buds to vegetative buds as a fourth correlate of development in these branches. Starting at the branch apex, we counted back towards the trunk until 200 vegetative buds were encountered or the branch was completely censused, whichever came first. We then worked back towards the apex, counting the number of reproductive buds or scars. Side branches were completely censused. The number of flowers per 200 vegetative buds was tabulated for all branches.

We tested the relationship between developmental distance and these branch characters in two ways. First, we used Pearson's r to determine the sign (positive or negative) of the relationship between these characters and developmental distance within each tree. Second, we tested the overall significance of the relationship across all trees by using an analysis of covariance with tree as an effect and developmental distance as a covariate.

We also compared the predictive power of developmental distance with that of branch height alone. If branch height, the distance from the ground to the point on the trunk where the branch was inserted, was a better predictor of leaf and reproductive characters, it could indicate that character change is a function of limitations of water translocation to the shoot simply against gravity, and the cost of supporting the intervening woody tissues. If developmental distance was a better predictor, it would indicate that hormonal gradients, hydraulic architecture, or ontogenetic mechanisms might be responsible.

To test between these possibilities, we performed a series of two-step stepwise analyses of covariance of morphological character and aphid density and resistance data from all 12 trees. For each character, we included clone as a factor in the first step of the model. At the second step we included either developmental distance or branch height as a covariate. We then compared the sequential sum of squares (SSS), the additional variation accounted for by the second character, of developmental distance to that of branch height. The factor with the higher SSS was considered a better predictor.

Effects of within-plant gradients on aphids

Because the performance of *Pemphigus* aphids was known to be related to host developmental stage differences among ramets of the same clone (Kearsley and Whitham 1989), we quantified variation in resistance to the aphids among branches of the same ramet by recording the density and survivorship of naturally occurring stem mothers on the same 10 branches of each ramet. For each of 20 shoots per branch, we recorded the number of first-flush leaves and the number of successful and aborted galls on all leaves of the shoot. These numbers were then used to describe aphid density (galls + scars per 1000 leaves), and survivorship [(galls)/(galls + scars)]. We used this bioassay of aphid performance in the following tests of the "distance hypothesis" of the developmental stream.

We compared resistance of branches with the same two methods used for the morphological correlates. First, within each ramet, we assessed the relationship between aphid density and developmental distance with Pearson's r . Percentage survivorship, after being arcsine transformed, was analyzed in the same way. As with the morphological traits, the significance of the resistance trait correlations across all trees was mea-

sured with an analysis of covariance. We also compared the predictive power of developmental distance vs. branch height with the same two-step analysis of covariance.

We tested for the stability of both morphological and resistance characters between years. Within a 16-m tall tree, we measured leaf width, length, and area, as well as aphid densities and survivorship during two consecutive years in 24 of its branches. We used Pearson's r to test the strength of the relationships between years.

Experimental examination of aphid fitness

To experimentally examine these patterns of within-plant development and its effects on aphid fitness, we performed a set of aphid transfers to one juvenile and one mature branch in each of 12 mature ramets in separate clones. Leaf morphology and branch reproduction measurements were taken as described above.

For the transfer experiment, overwintering eggs were collected from a single source tree in early April. As fundatrices emerged, they were transferred onto the trees. Approximately 60 fundatrices were transferred to each ramet; 30 were placed on shoots on a juvenile zone branch (<1.5 m trunk distance, no flowering buds present) and the rest on shoots on a mature zone branch (>4.0 m trunk distance, flower buds present). These branches and adjacent control branches were matched for aspect and bud phenological state and had been isolated from colonizing fundatrices from elsewhere on the tree with a sticky barrier.

In early June, after gall development was completed but before gall dehiscence and aphid migration to the secondary hosts, we returned to census the control and transfer branches for aphid fitness measures. We scored leaves for the presence of successful galls and aborted gall scars. Survivorship was defined as the percentage successful galls [galls/(galls + scars)]. The 10 largest galls on each branch were collected on dry ice for measures of fecundity. We compared survival on juvenile and mature branches with a Wilcoxon sign rank test, and compared fecundity (progeny per gall) and expected fitness (survivorship \times mean fecundity) with a paired t test.

RESULTS

Morphological correlates of development

Within ramets, morphological variation was large and correlated with developmental distance. All leaf and reproductive characters displayed significant, positive within-ramet changes with increasing distance from the root crown (Table 1). For ramets in all 12 clones, leaf blades became wider with developmental distance; blade width to length ratios increased significantly ($n = 10$ branches per ramet, $r = 0.67-0.95$; $P < 0.05$ for individual ramets). Similarly, petioles were relatively longer on shoots in the upper sections of ramets; petiole length to blade length ratios increased

TABLE 1. Correlation coefficients of characters with developmental distance.

Clone†	<i>r</i> between developmental distance and			
	Flowers per 200 shoots	Blade width/length	Petiole length/blade length	Leaf area‡
BPIT (1)	0.57	0.84	0.94	NA
CCLO (2)	0.64	0.90	0.59	NA
EXPA (3)	0.55	0.89	0.74	0.82
FCLO (4)	0.82	0.82	0.93	NA
FENS (5)	0.77	0.93	0.96	NA
HNEX (6)	0.93	0.91	0.83	NA
KCLO (7)	0.94	0.95	0.94	0.93
LEAN (8)	0.82	0.85	0.97	NA
LONE (9)	0.93	0.67	0.73	0.67
PNEX (10)	0.93	0.93	0.90	0.87
T120 (11)	0.97	0.88	0.67	NA
VNAR (12)	0.69	0.75	0.66	0.76
ANCOVA§	126.8	236.7	212.0	145.6
df	1, 107	1, 107	1, 107	1, 44
<i>P</i>	***	***	***	***
Factor	D > H	D > H	D > H	D > H

*** $P < 0.0001$.

† Numbers in parentheses refer to those used in Figs. 2 and 3.

‡ NA = measures not available due to loss of sample.

§ *F* values from the ANCOVA to test the overall significance of the relationship (i.e., correlation) across all trees. Clone was the effect in the ANCOVA and developmental distance was a covariate.

|| Comparisons of the sequential sums of squares (SSS) from developmental distance (D) and branch height (H). The factor with the higher SSS was considered a better predictor (see *Methods: Morphological correlates of development* for details).

significantly with developmental distance for all 12 ramets ($n = 10$ branches per ramet, $r = 0.59$ – 0.97 ; $P < 0.05$ for individual ramets). Mean leaf areas also increased with developmental distance. Samples from 7 of the 12 trees were lost in a drying oven mishap, but the remaining 5 trees all produced significant, positive correlations between developmental distance and leaf area (Table 1; $r = 0.66$ – 0.93 ; $P < 0.05$ for individual trees).

Also, more reproductive buds were produced by shoots in the higher parts of ramets (Table 1). The reproductive effort of shoots on branches was strongly, positively correlated with developmental distance ($n = 10$ branches per ramet, $r = 0.55$ – 0.97 ; $P < 0.05$ for individual ramets). Within the first 3 m of trunk and branch growth, no flowers were produced. Above that point, all branches showed a linear increase in reproduction.

An overall test for the significance of these correlations across all clones was highly significant in all cases. The analyses of covariance across all clones for these traits were all significant at $P < 0.001$ (Table 1). Thus, shoots at greater distances from the root crown express more mature phenotypes.

Natural aphid attack rates and survivorship

In addition to developmentally based variation within ramets in morphology, we found the same pattern of variation in *Pemphigus betae* attack rates and survivorship. Aphid densities increased with developmental distance in 8 of 12 trees (Fig. 2; $r = 0.52$ – 0.88). The analysis of covariance showed that the relationship between aphid density and developmental distance was significant across all clones ($F_{1,107} = 37.1$, $P < 0.001$). Thus, aphid colonization was highest in branches where shoots were expressing more mature phenotypes.

The resistance characters of shoots at greater growth distances from the root crown resembled our whole-ramet measures of mature plants as well. The survivorship of the fundatrices also showed a positive relationship with developmental distance in 8 of the 12 trees (Fig. 3; $r = 0.52$ – 0.89). One of the trees (LONE; Clone 9) could not be analyzed because the clone was extremely resistant and all aphid colonizers died. Overall, the analysis of covariance showed that the survival of colonizing stem mothers was strongly related to developmental distance ($F_{1,104} = 23.6$, $P < 0.001$).

Both morphological and resistance characters remained stable over a 2-yr period. Relative leaf blade widths in the 2nd yr were significantly, positively correlated with those in the 1st yr (Fig. 4A; $r = 0.75$, $n = 24$, $P < 0.01$). Leaf areas, likewise remained stable (Fig. 4B; $r = 0.85$, $n = 24$, $P < 0.01$). Most importantly, aphid densities and survival rates in the 2nd yr were positively correlated with those in the 1st yr (Fig. 4C; $r = 0.75$, $n = 24$, $P < 0.01$; Fig. 4D; $r = .57$, $n = 24$, $P < 0.01$), despite a nearly 50% reduction in the population size in the 2nd yr (Fig. 4C).

Developmental distance vs. branch height

Changes in leaf size and shape and branch reproductive output are better explained by developmental distance than branch height (Table 1). Comparing the sequential sums of squares (SSS), developmental distance explained 20% more of the variation in branch reproduction (SSS = 0.8471 vs. 0.7098) than branch height. Likewise, it better explained both relative blade width (SSS = 117 641 vs. 117 418) and relative petiole length (SSS = 0.3622 vs. 0.3325) than branch height, although only marginally so in the case of relative blade width. In the five ramets where data was available, developmental distance was a better predictor of leaf area than branch height (SSS = 145.7 vs. 111.9).

Pairs of adjacent branches in clone 3 (EXPA) demonstrate this clearly. Like branch B and the branch opposite in Fig. 1, branches 1 and 2 are inserted at nearly the same point on the trunk (1.25 and 1.35 m, respectively). However, branch 1 has a longer developmental distance (3.7 vs. 2.9 m) and also wider leaves (branch width/branch length = 0.40 vs. 0.38), longer petioles (petiole length/branch length = 1.9 vs. 1.7), larger average leaf area (8.3 vs. 7.3 cm²), and higher

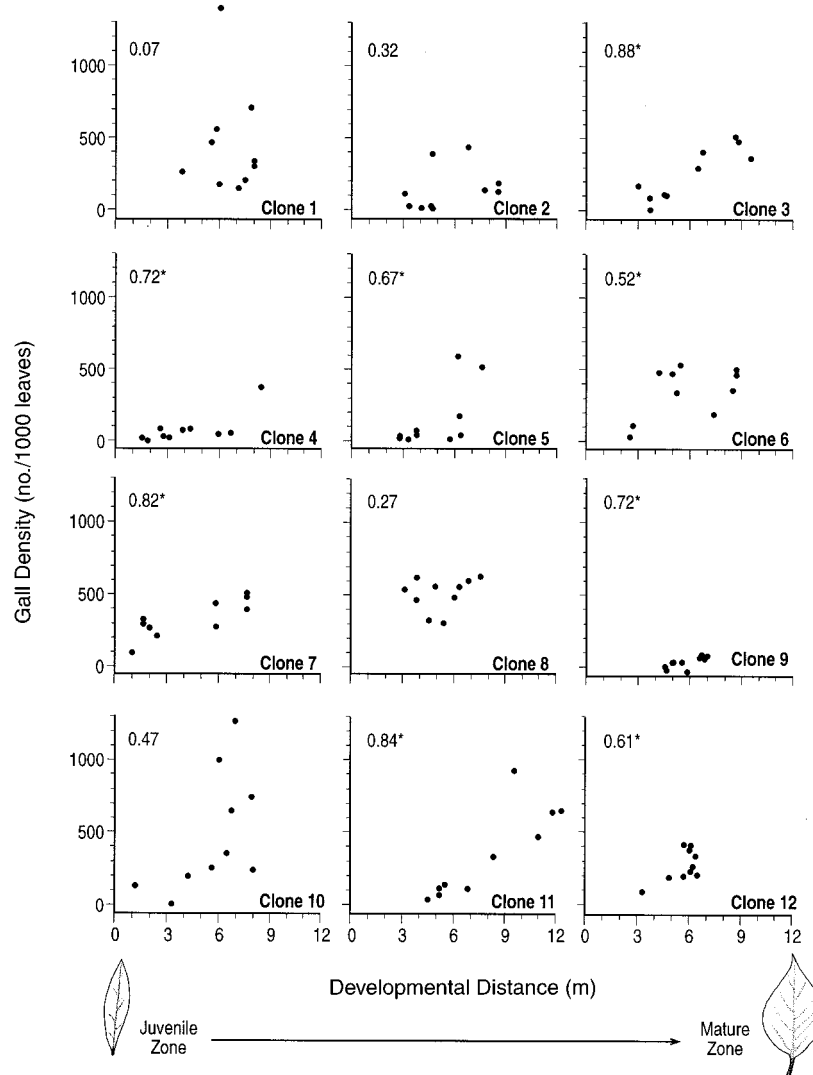


FIG. 2. Correlations of aphid densities with developmental distance in 12 mature cottonwood trees show that colonization changes with distance from the root crown. Clone numbers are identified in Table 1. Each point represents the census of 20 vegetative shoots within a branch; $n = 10$ branches per ramet. Numbers on each graph are simple correlation coefficients; * $P < 0.05$.

rates of flowering (5 vs. 2 flowers/200 vegetative shoots).

The patterns of aphid density and survival showed contrasting patterns when we compared developmental distance and branch height as predictors. Developmental distance explained marginally less variation in aphid density than branch height (sss = 1.2197 vs. 1.2751). However, developmental distance explained 10% more variation in stem mother survival than branch height (sss = 0.7625 vs. 0.6995), after the effect of clone was accounted for.

Experimental aphid transfers

Comparing mature- and juvenile-zone branches of the 12 transfer trees, we found the same pattern of increasingly mature shoot phenotypes of shoots on

branches with increasing developmental distance in the transfer trees. Shoots from higher branches had leaf morphologies more like mature ramets and shoots on lower branches had leaves more like those found on juvenile ramets of the same clone (Fig. 5). Juvenile zone leaves were ~20% narrower (mean blade width/length ratio = 0.36 vs. 0.30) than those in the mature zone of the same tree (Fig. 5B; $n = 12$, paired $t = 4.79$, $P < 0.001$). Juvenile branch leaves also had relative petiole lengths 50% shorter (mean petiole length/blade length ratio = 0.16 vs. 0.25) than mature zone leaves in the same trees (Fig. 5C; $n = 12$, paired $t = 3.78$, $P < 0.001$). By definition, none of the juvenile zone branches had flowers and all mature zone branches had some degree of flowering (Fig. 5A).

Leaf areas of the aphid transfer branches also showed

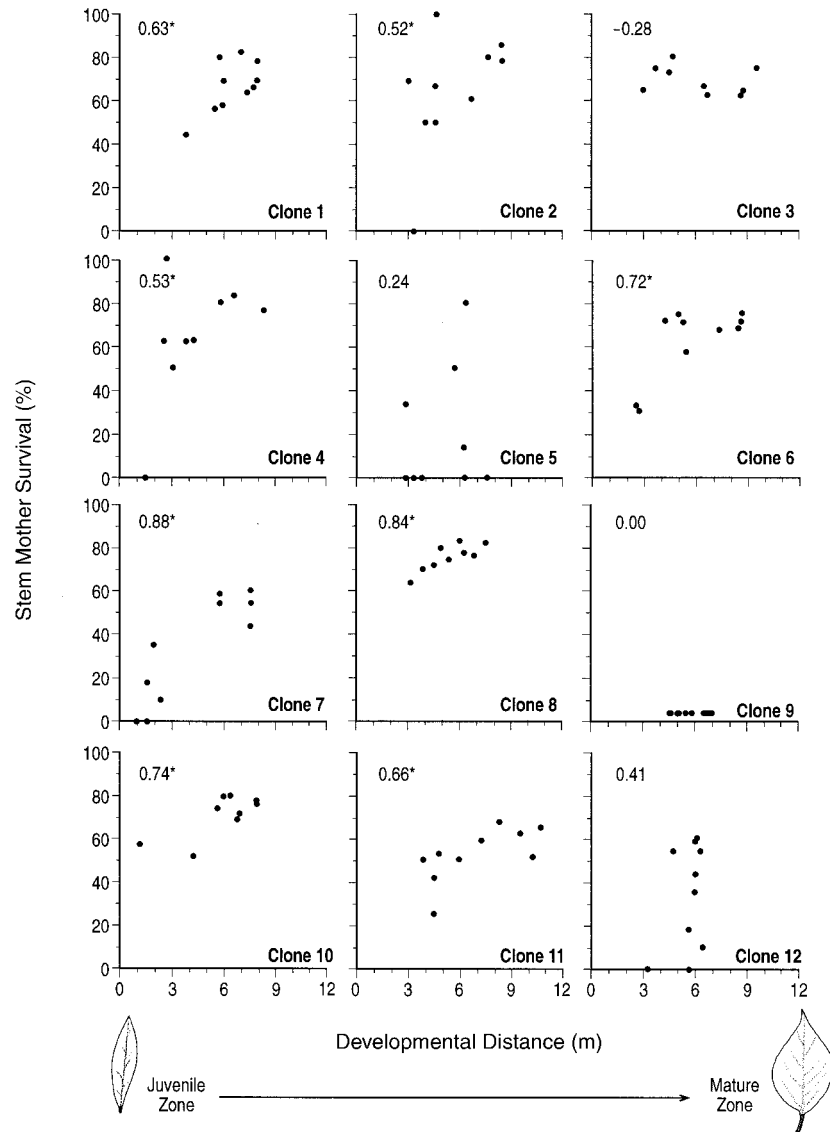


FIG. 3. Correlations of aphid survival with developmental distance in 12 mature cottonwood trees show that resistance changes with distance from the root crown. Clone numbers are identified in Table 1. Each point represents galls and abort scars encountered in 20 vegetative shoots per branch; $n = 10$ branches per ramet. Numbers on each graph are simple correlation coefficients; * $P < 0.05$

a pattern predicted by the distance hypothesis. Shoots from branches higher in the trees had leaves nearly 50% larger (11.5 cm^2 vs. 8.0 cm^2) than shoots from lower zone (Fig. 5D; $n = 12$, paired $t = 6.17$, $P < 0.001$). Within trees, differences ranged from 7% (9.5 cm^2 vs. 8.9 cm^2) to >70% (14 cm^2 vs. 8.2 cm^2).

Most importantly, aphid performance was significantly affected by developmental variation within individuals. Shoots on branches that express more mature phenotypes are more susceptible to attack than shoots on more juvenile branches of the same ramet. The survival of stem mothers was, with one exception, higher at greater developmental distances (Fig. 6A; $n = 12$, paired $t = 2.50$, $P < 0.025$). Survival was up to 65%

higher in mature zones of trees (89 vs. 55%), and averaged roughly one-third higher (77 vs. 58%) than on shoots in lower zones. Likewise, aphid fecundity was, with one exception, higher on shoots of mature zone branches (Fig. 6B; $n = 12$, paired $t = 5.06$, $P < 0.001$). In one tree, fecundity was 2.3 times higher on the mature zone branch (47 vs. 20 progeny/gall). Overall, fecundity was 50% higher in the mature zone.

The expected fitness of stem mothers, measured as average survival times mean progeny per survivor for each branch, was profoundly affected by developmentally based variation within individual ramets. The expected number of progeny per transferred female was significantly higher in the mature zone (Fig. 6C; $n =$

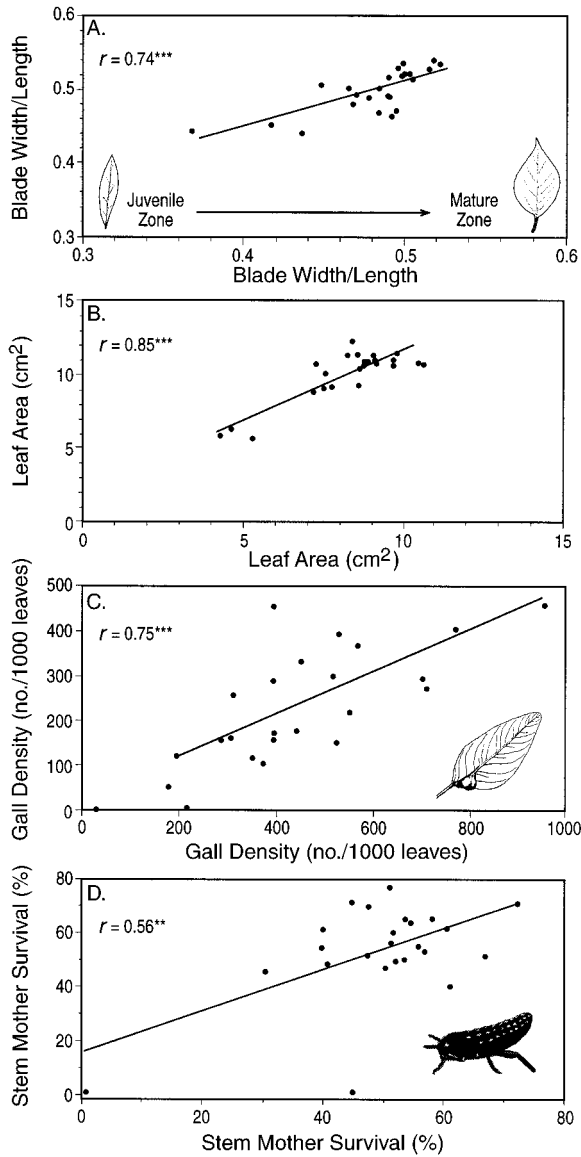


FIG. 4. Data from different branches of a single 16-m ramet show that cottonwood morphological traits and aphid preference and performance remained stable from one year to the next. Mean values per branch are presented for (A) leaf shape, (B) leaf area, (C) aphid density, and (D) mortality traits for all 24 major branches of tree number 999. Each point represents the means of measures from 10 to 40 shoots per branch. ** $P > 0.01$, *** $P < 0.001$.

12, paired $t = 6.77$, $P < 0.001$), ranging up to more than a factor of three (22 vs. 7 progeny/colonist). Overall, stem mothers realized more than an 80% higher number of offspring (55 vs. 30 offspring) on a mature zone branch than on a juvenile zone branch of the same ramet. Therefore, within a host ramet, where genetic and microsite factors are similar, if not identical, shoots with more mature phenotypes are better resource for aphids.

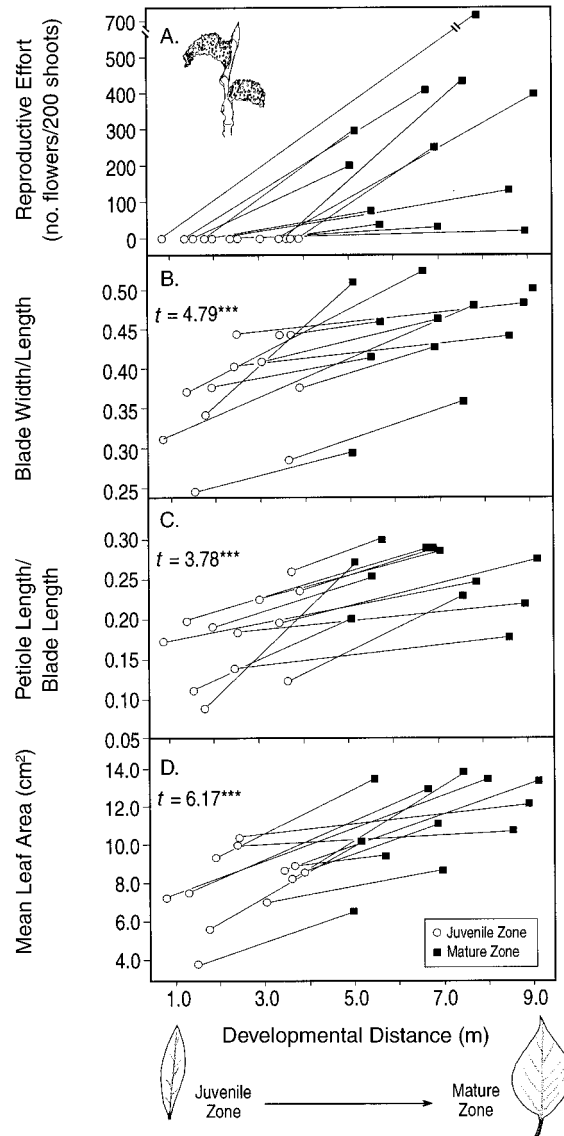


FIG. 5. Comparisons of morphological and reproductive traits in the 12 experimental transfer ramets from different clones show that, within ramets, shoots at greater developmental distances have more mature appearances. As depicted in Fig. 1, mature zone branches have shoots with (A) more reproductive shoots, (B) relatively wider leaves, (C) relatively longer petioles, and (D) relatively larger leaves. Open circles (○) represent juvenile zone branches, solid squares (■) show mature zone branches, and lines connect branches from the same ramet. The t statistics are from paired t tests, each with $n = 12$ trees. *** $P < 0.001$.

DISCUSSION

A mechanistic tie between development and resistance

Individual modules within a mature tree can express varying levels of maturity in patterns that are consistent with a developmental stream model. The distance from the root crown to the average shoot on a branch was

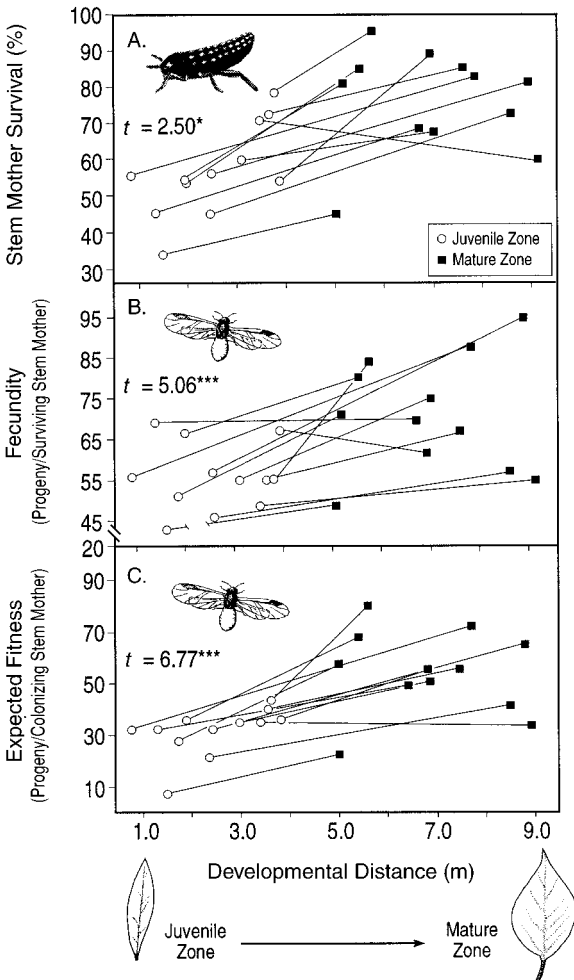


FIG. 6. The performance of aphids transferred to branches in the 12 experimental transfer ramets shows that the pattern of branch selection by aphids is adaptive; survival and reproduction are highest on branches in the mature zone. Open circles (○) represent juvenile zone branches, solid squares (■) represent mature zone branches, and lines connect branches from the same ramet. Survival data represent measures based on ~30 aphid fundatrices. Fecundity measures are based on 10 galls/branch. Expected fitness is the product of survival and fecundity. The t statistics are from paired t tests, each with $n = 12$ trees. * $P < 0.05$, *** $P < 0.001$.

highly correlated with both shoot reproductive effort and characteristics of leaf size and shape associated with increasing age (Kearsley and Whitham 1989 and unpublished data). This would explain the seemingly anomalous situations in which long, hanging branches that touch the ground but insert at midheight on the trunk, will exhibit mature traits, while shorter branches inserting lower will appear more juvenile.

We also demonstrated that, within ramets, resistance to aphids is affected by the developmental stream. The density and performance of naturally occurring *Pemphigus betae* aphids are highest on branches where shoots express the most mature phenotypes. Also, the

expected fitness of aphids experimentally transferred to mature branches was, on average, 80% higher than that of stem mothers transferred to juvenile branches (Fig. 6C). Although these within-plant patterns of developmental resistance changes are known for some plant pathogens (Soegaard 1956, Zagory and Libby 1985, Greenwood and Hutchison 1993 and references therein), this is the first case where it has been documented for an insect herbivore.

Because cloning experiments show that stecklings (field-grown rooted cuttings) from the top, middle, and bottom of a tree maintain their respective morphological and aphid resistance characters (Kearsley 1991 and unpublished data), the developmental variation we have described is likely ontogenetic, i.e., the result of differential gene activity through time. Furthermore, aphid sensitivity to plant developmental processes is likely due to the effects of plant development on the pattern of vascular flow and sink-source relationships that aphids utilize when feeding from phloem. The facts that (1) aphids perform best on large phloem sinks (large leaves), (2) compete with natural plant sinks such as flowers for plant resources, and (3) are affected by the density of neighboring buds as natural sinks (Larson 1989, Larson and Whitham 1991, 1997), all of which are under developmental control, provide a mechanistic explanation for why aphids are so closely tied to the developmental stream. Our observation that aphid densities are predicted by branch height better than by developmental distance is probably caused by either the aphid not having a means to distinguish between branch height and maturation distance or that their response to within-plant developmental gradients is simply to climb upward during colonization to where, on average, shoots are more susceptible.

Alternate sources of within-plant variation

Although leaf specific mass (mass per area) and xylem vessel characters are known to vary with maturational state in other systems (Hutchison et al. 1990, Takemoto and Greenwood 1993), we do not believe these would affect the types of herbivores discussed in this paper. First, *P. betae* fundatrices begin gall formation as soon as cracks appear between scales of unfolding buds. Thus, fundatrice survival and the success or failure of gall formation take place long before leaf size and thickness become significant. And second, *P. betae* is a phloem feeder, and not likely to be affected by changes to the xylem. Within-plant variation in such traits as leaf specific mass, toughness, and water content are likely to be the cause of clumping of other herbivores in this system, including free-feeding beetles (Kearsley 1991) and others (Waltz and Whitham 1997).

These patterns are not likely to be caused by non-developmentally based mechanisms. Within-ramet variation resulting from somatic mutations is not apt to vary as predictably as developmental processes

(Whitham and Slobodchikoff 1981). Rather, such variation would most likely produce a pattern in which morphology and resistance varied randomly with distance from the root crown, and/or differently for each trait studied (Whitham and Slobodchikoff 1981, Whitham et al. 1984). Nor are these patterns likely to be the result of shading of lower branches or difficulties in translocating water to upper branches. Greater levels of shading have been shown to produce leaves that are generally larger in lower levels of the canopy, and "sun leaves" at the top of the canopy tend to be smaller (Ashby 1948, Givnish 1978), although these effects can be limited to later flush leaves in heterophyllous species (Roy et al. 1986). Our data show larger leaves, rather than smaller leaves, higher in the canopy where light levels are highest. Water stress in cottonwoods produces shoots with marginally smaller leaves in stockings growing in dry sites (M. J. C. Kearsley and T. G. Whitham, *personal observations*). Thus shoots at greater distances from the root crown, where water stress is highest (Zimmermann 1982, Tyree et al. 1991, Joyce and Steiner 1995) should have similar-sized rather than larger leaves.

Several facts argue against these patterns being the result of variation induced by aphid feeding (i.e., Marshall 1989, Tuomi et al. 1989, Karban and Niiho 1995). If induction produces these consistent and graded within-plant patterns, herbivore levels must remain consistently high to regulate resource quality (e.g., Craig et al. 1988, Karban and Niiho 1995), and/or the induction of low quality by herbivore feeding must be maintained for several years (Karban 1987, Tuomi et al. 1988). However, herbivore levels fluctuate widely over relatively short time spans in this system (Whitham 1989) so that any effects of one year's herbivore damage would have to carry over for several years. But repeated sampling of the same branches shows that branches with high aphid survivorship in one year have high survivorship in subsequent years (Fig. 4C, D), regardless of the previous years' aphid densities. An hypothesis of induced susceptibility (Craig et al. 1986) would predict that the chronologically youngest tissues at the top of the tree would be the most resistant, in contrast to the pattern we have reported here.

We do not believe that developmental mechanisms are the only sources of within-plant host quality variation in this system (Whitham 1983, Williams and Whitham 1986, Moran and Whitham 1990, Larson and Whitham 1991, 1997, Floate and Whitham 1993). We see the developmental stream as an adjunct rather than an alternative to other sources of variation. However, the data presented here indicate that much of the morphological and resistance variation within a ramet can result from developmental processes.

Growth rules and the developmental stream

Development, especially in cases of the ontogenetic activation and repression of genes in long-lived species

(Takemoto and Greenwood 1993), results in an ordered, predictable change in the behavior of modules through time. The behavior of modules depends on their growth distance from the root crown. Thus, a developmental stream model predicts within-ramet variation in module behavior both within years and through time.

In contrast to the reality of developmentally based variation, mathematical models of plant growth begin by assuming the modular nature of plants, but have often assumed either constant or stochastic module behavior (Bell et al. 1979, Harper 1981, White 1984, Berger 1991). Models that describe ground-covering vines as "horizontal trees" (e.g., Janzen 1975) based on constant morphological and growth rules, fail to recognize that important aspects of module behavior will change during an individual's growth as a result of development. Models based on stochastic module behavior (i.e., responses to shading and previous-year reproductive activity) (Harper 1977, 1989, Lindenmayer 1978, Bell 1984, Jones 1985, Roy et al. 1986, Cain and Cook 1988, McGraw 1989, Greenwood and Hutchinson 1993, Watson et al. 1995) do not account for the developmentally based limits on behavior in terms of module morphology, reproductive effort, and resistance characteristics.

Whole-tree maturity and insect resistance patterns

Because a tree is a population of individual shoots, (Harper 1977, 1981, Fagerström 1992), its overall developmental state is defined by the developmental states of its modules. Its form (size and shape) is the net product of the demography of these modules (Bell 1984, Jones 1985). Furthermore, because the developmental state of modules depends on their position relative to the root crown, the developmental stream will contribute to two important resistance characteristics of the tree as a whole.

First, for herbivores such as *P. betae*, which are sensitive to developmental changes in their hosts, the abundance of mature and juvenile shoots within their host will define the host's overall classification as resistant or susceptible. Studies such as our previous work (Kearsley and Whitham 1989), which estimate whole-ramet development, will define ramet-wide resistance based on *averages* of modules in different developmental states collected within that ramet. Genetically susceptible mature ramets would be classified as susceptible overall, even though they may contain some juvenile, more resistant modules in branches at their base.

Second, the variation in and patchiness of resource quality within ramets will be determined by the growth, proliferation, and death of modules throughout the tree's canopy over its life. When shoots are distributed uniformly throughout the trunk and canopy, herbivores will perceive a host plant as a fine-grained, gently graded environment. However, a more clustered distribution on long, terminal-heavy branches with long stretches

of trunk between branches will produce a much more coarse-grained, patchy array of resources. Therefore, although age-related variation in host quality is often dismissed as being the result of lost module vigor with increasing ramet size or separation from the roots (Zelazny and Pacumbaba 1982, Stephen and Wallis 1984, Price 1989), we see age-related, within-ramet variation in resistance as a dynamic part of the evolutionary interactions between herbivores and their hosts.

Evolutionary changes in plant resistance may often be viewed from a developmental standpoint as well. Studies on variation in the timing and duration of ontogenetic processes (heterochronic evolution; Wiltshire et al. 1991) have a long history in the literature of vertebrate evolution (Cope 1887:76–93) but in plants have focused primarily on morphological traits (Poethig 1990, Wiltshire et al. 1991). Developmentally based variation in resistance to herbivores should also be subject to the same type of selection. While the observed levels of *Pemphigus* aphids' impact on cottonwoods may not be sufficient to produce evolutionary pressures (Larson 1989; M. J. C. Kearsley and T. G. Whitham, unpublished data), the distribution of many other herbivores is correlated with aphid distribution (Whitham et al. 1991, Dickson and Whitham 1996), and together these may produce significant impacts on the fitness of their hosts.

Significance of developmentally based within-plant variation

The high degree of developmentally based within-ramet variation we have documented here has at least three further ecological implications. First, the *within-ramet* variation in morphology and resistance in this system can be nearly as great as among-ramet clonal effects (Keim et al. 1989, Whitham 1989). Within ramets, the amount of variation in reproductive output, relative petiole length, and leaf area explained by clone and maturation distance are similar (43 vs. 31%, 39 vs. 38%, and 28 vs. 20%, respectively). For relative blade width, gall density and stem mother survival, clonal effects account for more of the variation than maturation distance (70 vs. 15%, 55 vs. 25%, and 60 vs. 10%, respectively), but the latter does contribute significantly. Similar levels of within-plant variation have been reported in other systems for host chemistry (Suomela and Ayres 1994) and host quality (Suomela and Nilson 1994), although no distance-based patterns were noted.

Second, the propagation of long-lived plants for research or agricultural purposes (Schaffalitzky de Muckadell 1954, Nienstaedt 1961, Bolstad and Libby 1982, McGranahan and Forde 1985) must be done with the species' developmental stream in mind. Even when ramets are selected for their genetically-based resistance, architectural, fruiting, and other characteristics (Rouland 1973, 1979, Bolstad and Libby 1982, Greenwood 1984, McGranahan and Forde 1985, Greenwood et al.

1989), our data indicate that the location of shoots selected within a ramet should be standardized to control or capitalize on traits that vary developmentally. While this has been shown to be true for endophytic and pathogenic fungi (Soegaard 1956, Zagory and Libby 1985, Espinosa-Garcia and Langenheim 1990), the case for resistance to insect herbivores has not been made previously. Similarly, ecological sampling from individuals that have developmentally labile modules must be carried out with an understanding of the plants' developmental stream. Herbivore densities and survivorship on shoots from different levels of the crown of a single ramet can be affected by development to a very large degree.

Third, when developmental processes affect the distribution of common herbivores, they have the potential to influence community structure. In this system we find that the gall aphid *Pemphigus betae* is largely restricted to the mature zones of trees, while the leaf-feeding beetle *Chrysomela confluenta* is largely restricted to juvenile trees and juvenile zones of mature trees (Kearsley and Whitham 1989, Kearsley 1991). These insects in turn directly and indirectly affect community structure. For example, Waltz and Whitham (1997) found that aphid removal decreased arthropod species richness and abundance in mature zones by 32 and 55%, respectively, while beetle removal increased species richness and abundance on juvenile ramets by 120 and 75%, respectively. Even vertebrates and fungi are affected; Dickson and Whitham (1996) found that the removal of aphids caused a threefold decline in foraging by birds such as the Black-capped Chickadee, *Parus atricapillus*, and a twofold decline in the fungus *Cladosporium cladosporioides*. Furthermore, since heritability studies on *Eucalyptus* argue that the timing of the shift from juvenile to mature foliage is under genetic control (Wiltshire et al. 1992), different tree genotypes will exhibit different ratios of juvenile to mature foliage, which in turn will differentially affect the organisms dependent upon each habitat type. In total, these studies suggest that the indirect impacts of plant development acting through common herbivores may rival direct impacts (e.g., competition and predation) in their overall importance (Waltz and Whitham 1987). Thus, while the basic process of plant ontogeny and senescence have not generally been appreciated by ecologists, they are nevertheless likely to be important in understanding community-level processes.

We feel that the developmental streams of long-lived plants are important components of their ecological and evolutionary relationships with their herbivores. The protean nature of shoot behavior during a plant's lifetime should provide a platform from which hypotheses about the effects of plant variation can be tested. The long history of well-documented cases of developmentally based variation leads us to believe that such efforts will prove fruitful.

ACKNOWLEDGMENTS

This research was performed in partial fulfillment of the requirements of the Ph.D. degree at Northern Arizona University. We wish to thank T. P. Craig, R. Declerck-Floate, K. Floate, K. C. Larson, and P. W. Price for helpful advice at several stages of fieldwork and writing; N. Cobb, G. Martinson, B. Wade, and G. Wimp for comments on the manuscript; L. Kearsley and R. B. Kearsley for assistance in the field; R. Foust and E. Wong of the Bilby Research Center for logistical support; and Utah Power and Light Co./PacifiCorp for their generosity and hospitality. Reviews by P. B. Reich and two anonymous reviewers improved the manuscript. This work was supported by NSF grants BSR-9107042 and DEB-9408009, USDA grant 95-37302-1801, Department of Energy grant DE-F603-94ER61849, and NAU Organized Research Support grants to T. G. Whitham, and Sigma Xi, NAU Organized Research Support grants, and Bilby Research Center Support funds to M. J. C. Kearsley.

LITERATURE CITED

- Ashby, E. 1948. Studies in the morphogenesis of leaves. I. An essay on leaf shape. *New Phytologist* **47**:153–174.
- Bell, A. D. 1984. Dynamic morphology: a contribution to plant population ecology. Pages 48–65 in R. Dirzo and J. Sarukhan, editors. *Perspectives on plant population ecology*. Sinauer, Sunderland, Massachusetts, USA.
- Bell, A. D., S. Roberts, and A. Smith. 1979. Branching patterns: the simulation of plant architecture. *Journal of Theoretical Biology* **81**:351–375.
- Bennett, I. J., C. M. Tonkin, M. M. Wroth, E. M. Davison, and J. A. McComb. 1986. A comparison of growth of seedling and micropropagated *Eucalyptus marginata* (Jarrah). I. Early growth to 2 years. *Forest Ecology and Management* **14**:1–12.
- Berger, D. 1991. Modification of a simple fractal tree growth scheme: implications for growth variation, and evolution. *Journal of Theoretical Biology* **152**:513–529.
- Bolstad, P. V., and W. J. Libby. 1982. Comparisons of radiata pine cuttings of hedge and tree-form origin after seven growing seasons. *Silvae Genetica* **31**:9–13.
- Borchert, R., and N. A. Slade. 1981. Bifurcation ratios and the adaptive geometry of trees. *Botanical Gazette* **142**:394–401.
- Brink, R. A. 1962. Phase change in higher plants and somatic cell heredity. *Quarterly Review of Biology* **37**:1–22.
- Bryant, J. P. 1981. Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. *Science* **213**:889–890.
- Bryant, J. P., G. D. Wieland, P. B. Reichardt, V. E. Lewis, and M. C. McCarthy. 1983. Pinosylvan methyl ether deters snowshoe hare feeding on green alder. *Science* **222**:1023–1025.
- Cain, M. L., and R. E. Cook. 1988. Growth in *Medeola virginiana* clones. II. Stochastic simulation of vegetative spread. *American Journal of Botany* **75**:732–738.
- Cameron, R. J. 1970. Light intensity and the growth of *Eucalyptus* seedlings. I. Ontogenetic variation in *E. fasciata*. *Australian Journal of Botany* **18**:29–43.
- Caplan, A. I., and C. P. Ordahl. 1978. Irreversible gene repression model for control of development. *Science* **201**:120–130.
- Clancy, K. M., and P. W. Price. 1986. Temporal variation in three-trophic-level interactions among willows, sawflies, and parasites. *Ecology* **67**:1601–1607.
- Cope, E. D. 1887. *The origin of the fittest: essays on evolution*. Macmillan, New York, New York, USA.
- Craig, T. P., P. W. Price, and J. K. Itami. 1986. Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology* **67**:419–425.
- Craig, T. P., J. K. Itami, and P. W. Price. 1988. Plant wound compounds from oviposition scars used in host discrimination by a stem-galling sawfly. *Journal of Insect Behavior* **1**:343–356.
- Dickson, L. L., and T. G. Whitham. 1996. Genetically-based plant resistance traits affect arthropods, fungi, and birds. *Oecologia (Berlin)* **106**:400–406.
- Eckenwalder, J. E. 1984. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections Aigeiros and Tacamahaca. II. Taxonomy. *Canadian Journal of Botany* **62**:325–335.
- Espinosa-Garcia, F. J., and J. H. Langenheim. 1990. The endophytic fungal community in leaves of a coastal redwood population—diversity and spatial patterns. *New Phytologist* **116**:89–97.
- Fagerström, T. 1992. The meristem–meristem cycle as a basis for defining fitness in clonal plants. *Oikos* **63**:449–453.
- Floate, K. D., and T. G. Whitham. 1993. The “hybrid bridge” hypothesis: host shifting via plant hybrid swarms. *American Naturalist* **141**:651–662.
- Foggo, A., M. R. Speight, and J. C. Gregoir. 1994. Root disturbance of common ash, *Fraxinus excelsior* (Oleaceae) leads to reduced foliar toughness and increased feeding by a folivorous weevil, *Stereonychus fraxini* (Coleoptera, Curculionidae). *Ecological Entomology* **19**:344–348.
- Fortanier, E. J., and H. Jonkers. 1976. Juvenility and maturity of plants as influenced by their ontogenetical and physiological ageing. *Acta Horticulturae* **56**:37–43.
- Givnish, T. J. 1978. Ecological aspects of plant morphology: leaf form in relation to environment. Pages 83–142 in R. Sattler, editor. *Theoretical plant morphology*. Leiden University Press, The Hague, The Netherlands.
- Green, T. R., and C. A. Ryan. 1972. Wound-induced proteinase inhibitor in plant leaves: a possible defense mechanism against insects. *Science* **175**:776–777.
- Greenwood, M. S. 1984. Phase change in loblolly pine: shoot development as a function of age. *Physiologia Plantarum* **61**:518–522.
- Greenwood, M. S., C. A. Hopper, and K. W. Hutchison. 1989. Maturation in larch. I. Effect of age on shoot growth, foliar characteristics, and DNA methylation. *Plant Physiology* **90**:406–412.
- Greenwood, M. S., and K. W. Hutchison. 1993. Maturation as a developmental process. Pages 14–33 in M. R. Ahuja and W. J. Libby, editors. *Clonal forestry. I. Genetics and biotechnology*. Springer-Verlag, New York, New York, USA.
- Haffner, V., F. Enjalric, L. Lardet, and M. P. Carron. 1991. Maturation of woody plants: a review of metabolic and genomic aspects. *Annales des Sciences Forestières* **48**:615–630.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, New York, New York, USA.
- . 1981. The concept of population in modular organisms. Pages 53–77 in R. M. May, editor. *Theoretical ecology*. second edition. Sinauer, Sunderland, Massachusetts, USA.
- . 1989. The value of a leaf. *Oecologia (Berlin)* **80**:53–58.
- Holliday, R., and J. E. Pugh. 1975. DNA modification mechanisms and gene activity during development. *Science* **187**:226–232.
- Hood, J. V., and W. J. Libby. 1978. Continuing effects of maturation state in radiata pine and a general maturation model. Pages 220–232 in K. W. Hughes, R. Henke, and M. Constantin, editors. *Propagation of higher plants through tissue culture: a bridge between research and application*. Technical Information Center, United States Department of Energy, Washington, D.C., USA.
- Hutchison, K. W., C. D. Sherman, J. Weber, S. Schiller Smith, P. B. Singer, and M. S. Greenwood. 1990. Maturation in

- larch. II. Effects of age on photosynthesis and gene expression in developing foliage. *Plant Physiology* **94**:1308–1315.
- Janzen, D. H. 1975. *Ecology of plants in the tropics*. Edward Arnold, London, England.
- Jones, M. 1985. Modular demography and form in silver birch. Pages 223–237 in J. White, editor. *Studies on plant demography*. Academic Press, New York, New York, USA.
- Joyce, B. J., and K. C. Steiner. 1995. Systematic variation in xylem hydraulic capacity within the crown of white ash (*Fraxinus americana*). *Tree Physiology* **15**:649–656.
- Karban, R. 1987. Herbivory dependent on plant age: a hypothesis based on acquired resistance. *Oikos* **48**:336–337.
- Karban, R., and C. Niiho. 1995. Induced resistance and susceptibility to herbivory: plant memory and altered plant development. *Ecology* **76**:1220–1225.
- Kearsley, M. J. C. 1991. The effects of host development on herbivores of narrowleaf cottonwood (*Populus angustifolia* L.). Dissertation. Northern Arizona University, Flagstaff, Arizona, USA.
- Kearsley, M. J. C. and T. G. Whitham. 1989. Developmental changes in resistance to herbivory: implications for individuals and populations. *Ecology* **70**:422–434.
- Keim, P., K. N. Paige, T. G. Whitham, and K. G. Lark. 1989. Genetic analysis of an interspecific hybrid swarm of *Populus*: occurrence of unidirectional introgression. *Genetics* **123**:557–565.
- Khait, A. 1986. Hormonal mechanisms for size measurement in living organisms in the context of maturing juvenile plants. *Journal of Theoretical Biology* **118**:471–483.
- Kramer, P. J., and T. T. Kozlowski 1979. *Physiology of woody plants*. Academic Press, New York, New York, USA.
- Larson, K. C. 1989. Sink-source interactions between a gall-forming aphid and its narrowleaf cottonwood host: within- and between-plant variation. Dissertation. Northern Arizona University, Flagstaff, Arizona, USA.
- Larson, K. C. and T. G. Whitham. 1991. Manipulation of food resources by a gall-forming aphid: the physiology of sink-source interactions. *Oecologia (Berlin)* **88**:15–21.
- Larson, K. C., and T. G. Whitham. 1997. The sink competition hypothesis: plant architecture affects resistance to gall aphids. *Oecologia*, (in press).
- Lawson, E. J. R., and R. S. Poethig. 1995. Shoot development in plants: time for a change. *Trends in Genetics* **11**:263–268.
- Libby, W. J., A. G. Brown, and J. M. Fielding. 1972. Effects of hedging radiata pine on production, rooting, and early growth of cuttings. *New Zealand Journal of Forest Science* **2**:263–283.
- Libby, W. J., and J. V. Hood. 1976. Juvenility in hedged radiata pine. *Acta Horticulturae* **56**:91–98.
- Lillie, F. R. 1927. The gene and the ontogenetic process. *Science* **66**:361–368.
- Lindenmayer, A. 1978. Algorithms for plant morphogenesis. Pages 37–82 in R. Sattler, editor. *Theoretical plant morphology*. Leiden University Press, The Hague, The Netherlands.
- Longman, K. A., and P. F. Wareing. 1959. Early induction of flowering in birch seedlings. *Nature (London)* **184**:2037–2038.
- Marshall, D. L. 1989. Integration of response to defoliation within plants of two species of *Sesbania*. *Functional Ecology* **3**:207–214.
- McGranahan, G., and H. I. Forde. 1985. Relationship between clone age and selection trait expression in mature walnuts. *Journal of the American Society for Horticultural Science* **110**:692–696.
- McGraw, J. B. 1989. Effects of age and size on life history and population growth of *Rhododendron maximum* shoots. *American Journal of Botany* **76**:113–123.
- Moran, N. A., and T. G. Whitham. 1988. Evolutionary reduction of complex life cycles: loss of host-alternation in *Pemphigus* (Homoptera: Aphididae). *Evolution* **42**:717–728.
- Moran, N. A., and T. G. Whitham. 1990. Differential colonization of resistant and susceptible host plants: *Pemphigus* and *Populus*. *Ecology* **71**:1059–1067.
- Nienstaedt, H. 1961. Induction of early flowering: a critical review of recent literature. Pages 1658–1662 in *Recent advances in botany*. Volume 2. University of Toronto Press, Toronto, Ontario, Canada.
- Poethig, R. S. 1990. Phase change and the regulation of shoot morphogenesis in plants. *Science* **250**:923–930.
- Price, P. W. 1989. Clonal development of coyote willow, *Salix exigua* (Salicaceae), and attack by the shoot-galling sawfly, *Euura exiguae* (Hymenoptera: Tenthredinidae). *Environmental Entomology* **18**:61–68.
- Price, P. W., and K. M. Clancy. 1986. Multiple effects of precipitation on *Salix lasiolepis* and populations of the stem-galling sawfly, *Euura lasiolepis*. *Ecological Research* **1**:1–14.
- Price, P. W., H. Roininen, and J. Tahvanainen. 1987a. Plant age and attack by the bud galler, *Euura mucronata*. *Oecologia (Berlin)* **73**:334–337.
- Price, P. W., H. Roininen, and J. Tahvanainen. 1987b. Why does the bud-galling sawfly, *Euura mucronata*, attack long shoots? *Oecologia (Berlin)* **74**:1–6.
- Remphry, W. L., and G. R. Powell. 1982. Crown architecture of *Larix laricina* saplings: an analysis of higher order branching. *Canadian Journal of Botany* **65**:268–279.
- Robbins, W. J. 1957. Gibberellic acid and the reversal of adult *Hedera* to a juvenile state. *American Journal of Botany* **44**:743–746.
- Roininen, H., P. W. Price, and J. Tahvanainen. 1988. Field test of resource regulation by the bud-galling sawfly, *Euura mucronata*, on *Salix cinerea*. *Holarctic Ecology* **11**:136–139.
- Roulund, H. 1973. The effect of cyclophysis and topophysis on the rooting ability of Norway spruce cuttings. *Forest Tree Improvement* **5**:21–41.
- . 1979. Stem form of cuttings related to age and position of scions. (*Picea abies* L. karst.). *Forest Tree Improvement* **13**:1–24.
- Roy, J., B. Thiebaut, and M. A. Watson. 1986. Physiological and anatomical consequences of morphogenic polymorphism: leaf response to light intensity in young beech trees (*Fagus sylvatica* L.). Pages 431–449 in *Natural history of the Colloque International sur l'Arbre*. Institut de Botanique, Montpellier, France.
- Schaffalitzky de Muckadell, M. 1954. Juvenile stages in woody plants. *Physiologia Plantarum* **7**:782–796.
- . 1956. Experiments on development in *Fagus sylvatica* by means of herbaceous grafting. *Physiologia Plantarum* **9**:396–400.
- Soegaard, B. 1956. Leaf blight resistance in thuja. Experiments on resistance to attack by *Didymascella thujina* (dur.) Maire (*Keithia thujina*) on *Thuja plicata* Lamb. *Kongelige Veterinaer-og Landbohojskole Asskrift (yearbook)*:30–48.
- Steele, M. J., M. P. Coutts, and M. M. Yeoman. 1989. Developmental changes in Sitka spruce as indices of physiological age. I. Changes in needle morphology. *New Phytologist* **113**:367–375.
- Stephen, F. M., and G. W. Wallis. 1984. Dynamics of nantucket pine tip moth populations in intensively managed pine plantations in Arkansas. *Proceedings of the International Union of Forest Research Organization (IUFRO) Conference, September 1980, Dornoch, Scotland*. Kom-

- missionsverlag Buchhandlungen Max Wiedebusch Hamburg, Germany.
- Suomela, J., and M. P. Ayres. 1994. Within-tree and among-tree variation in leaf characteristics of mountain birch and its implications for herbivory. *Oikos* **70**:212–222.
- Suomela, J., and A. Nilson. 1994. Within- and among-tree variation in growth of *Epirrita autumnata* on mountain birch leaves. *Ecological Entomology* **19**:45–56.
- Takemoto, Y., and M. S. Greenwood. 1993. Maturation in larch: age-related changes in xylem development in the long-shoot foliage and the main stem. *Tree Physiology* **13**: 253–262.
- Tallamy, D. W. 1985. Squash beetle feeding behavior: an adaptation against cucurbit defenses. *Ecology* **66**:1574–1579.
- Tuomi, J., P. Niemela, I. Jussila, T. Vuorisalo, and V. Jormalainen. 1989. Delayed budbreak: a defensive response of mountain birch to early-season defoliation? *Oikos* **54**: 87–91.
- Tuomi, J., T. Vuorisalo, P. Niemela, S. Nigula, and V. Jormalainen. 1988. Localized effects of branch defoliations on weight gains of female inflorescences in *Betula pubescens*. *Oikos* **51**:327–330.
- Tyree, M. T., D. A. Snyderman, T. R. Wilmot, and J.-L. Machado. 1991. Water relations and hydraulic architecture of a tropical tree (*Schefflera morotoni*): data, models, and a comparison with two temperate species (*Acer saccharum* and *Thuja occidentalis*). *Plant Physiology* **96**:1105–1113.
- Waltz, A. M., and T. G. Whitham. 1997. Plant development affects arthropod community structure: opposing impacts of species removal. *Ecology* **78**:2133–2144.
- Watson, M. A., M. A. Geber, and C. S. Jones. 1995. Ontogenetic contingency and the expression of plant plasticity. *Trends in Ecology and Evolution* **10**:474–475.
- White, J. 1984. Plant metamerism. Pages 15–47 in R. Dirzo and J. Sarukhan, editors. *Perspectives on plant population ecology*. Sinauer, Sunderland, Massachusetts, USA.
- Whitham, T. G. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. *Ecology* **59**:1164–1176.
- . 1983. Host manipulation of parasites: within-plant variation as a defense against rapidly evolving pests. Pages 15–41 in R. F. Denno and M. S. McClure, editors. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, New York, USA.
- . 1989. Plant hybrid zones as sinks for pests. *Science* **244**:1490–1493.
- Whitham, T. G., J. Maschinski, K. C. Larson, and K. N. Paige. 1991. Plant responses to herbivory: the continuum from negative to positive and underlying physiological mechanisms. Pages 227–256 in P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, editors. *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. John Wiley & Sons, New York, New York, USA.
- Whitham, T. G., and C. N. Slobodchikoff. 1981. Evolution by individuals, plant-herbivore interactions, and mosaics of genetic variability: the adaptive significance of somatic mutations in plants. *Oecologia (Berlin)* **49**:287–292.
- Whitham, T. G., A. G. Williams, and A. M. Robinson. 1984. The variation principle: individual plants as temporal and spatial mosaics of resistance to rapidly evolving pests. Pages 16–51 in P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, editors. *A new ecology: novel approaches to interactive systems*. John Wiley & Sons, New York, New York, USA.
- Williams, A. G., and T. G. Whitham. 1986. Premature leaf abscission: an induced plant defense against gall aphids. *Ecology* **67**:1619–1627.
- Wiltshire, R. J. E., B. M. Potts, and J. B. Reid. 1991. A paedomorphocline in *Eucalyptus*: natural variation in the *E. risdonii/E. tenuiramus* complex. *Australian Journal of Botany* **39**:545–566.
- Wiltshire, R. J. E., B. M. Potts, and J. B. Reid. 1992. A paedomorphocline in *Eucalyptus*. II. Variation in seedling morphology in the *E. risdonii/E. tenuiramus* complex. *Australian Journal of Botany* **40**:789–805.
- Zagory, D., and W. J. Libby. 1985. Maturation-related resistance of *Pinus radiata* to western gall rust. *Phytopathology* **75**:1443–1447.
- Zelazny, B., and E. Pacumbaba. 1982. Phytophagous insects associated with cadang-cadang infected and healthy coconut palms in south-eastern Luzon, Philippines. *Ecological Entomology* **7**:113–120.
- Zimmermann, M. H. 1982. Functional xylem anatomy of angiosperm trees. Pages 59–70 in P. Baas, editor. *New perspectives in wood anatomy*. Martinus Nijhoff/Dr. W. Junk, Boston, Massachusetts, USA.