THE DISCRIMINATION OF COTTONWOOD CLONES IN A MATURE POPULATION ALONG THE OLDMAN RIVER, ALBERTA

LORI A. GOM

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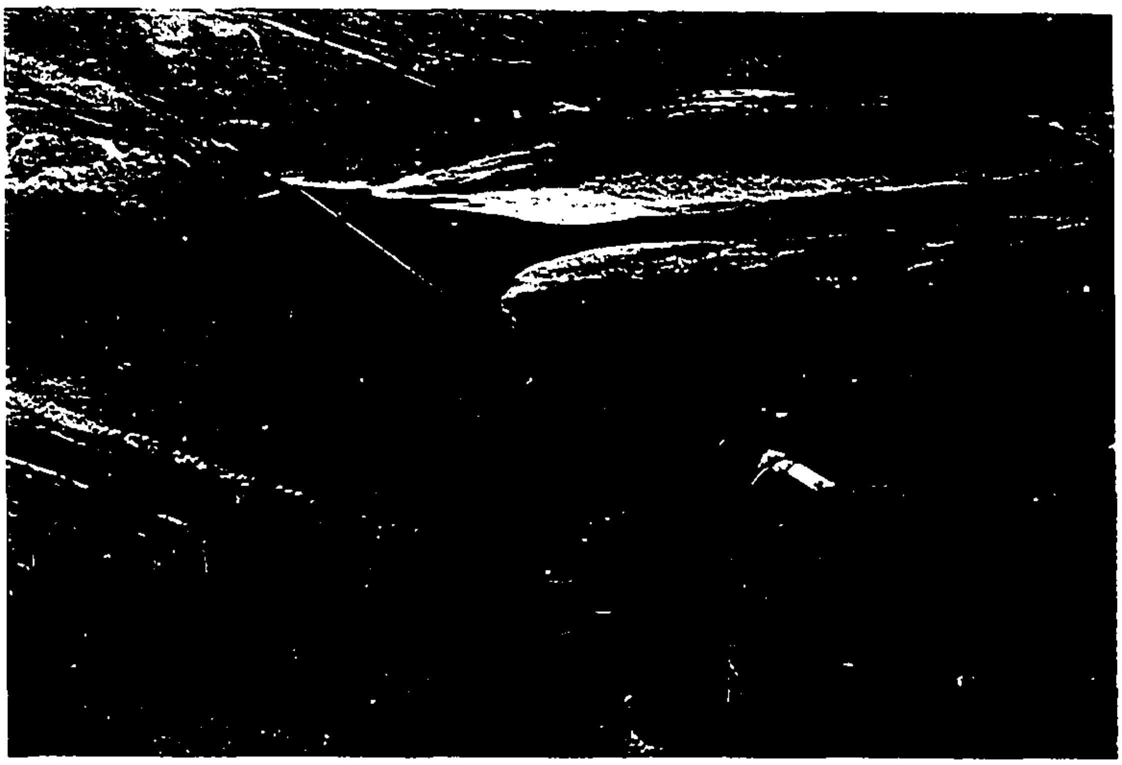

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ABSTRACT:

In the northwestern prairies, the cottonwoods *Populus deltoides* Bartr., *P. balsamifera* L., *P. angustifolia* James, and interspecific hybrids, form the foundation of the riparian forest ecosystem. The present project characterized the phenotype and phenology of each tree in a mature cottonwood grove (N=391) for the purposes of clone-delineation. In order of their utility, tree sex, general leaf-shape, six leaf dimensions, and phenology of flowering, leaf-flushing, senescence, and leaf-abscission were utilized. The population's 391 trunks represented only 115 individuals, 67 of which were clones which ranged from 2 to 58 trunks each. Thus, 88% of all trunks belonged to clones, and this high clonal content reflects the senior age of the population. Clone structure explained the population's apparent spatial-clumping, female-skewed sex ratio, differential spatial distributions of the sexes and species, and complexity in trunk-size classes. Trends suggest that *P. balsamifera* and *P. angustifolia* are more strongly clonal than *P. deltoides*, partially explaining their differences in environmental preferences. The observed extent of asexual regeneration has implications for riparian resource management and analyses of cottonwood reproductive ecology.

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1.1 Introduction to Riparian Cottonwoods:

1.1.1 Native species in Canada and Alberta:

Poplars, commonly known as cottonwoods, are widely distributed throughout the northern hemisphere and are abundant across North America. In Canada, they are well known trees because they are naturally abundant and are cultivated in every province. *Populus* species appear in most of the North American ecoclimatic regions. The dry conditions in south-central and southeastern Alberta have prohibited the growth of almost all trees, so the landscape is predominated by open treeless prairie. Occasionally these dry expanses are broken by river valleys with seasonally fluctuating stream flows fed by the runoff from local precipitation and snow melt from higher elevations. Unlike the open prairies, the river valleys are capable of supporting southern Alberta's native forests. Incorporating the term 'riparian' to describe zones associated with the banks of a watercourse, riparian forests are composed of a select group of tree species adapted to and dependant upon the river flow. These are the riparian cottonwoods. Of the five poplar species native to southern Alberta, four are the cottonwoods *Populus deltoides* Bartr. ex Marsh., *P. balsamifera* L., *P. trichocarpa* Torr. & Gray and *P. angustifolia* James, characteristic of riparian areas, and the fifth is the more upland aspen species, *P. tremuloides* Michx..

Populus deltoides is also known as the prairie, eastern, common, or plains cottonwood, and it belongs to the *Populus* Section *Aigeiros*. It is one of the largest poplars, with a champion specimen from Colorado measuring 3.4 meters in trunk diameter (Bronaugh 1993). Trunk diameters of 0.6 to 1.2 meters are more common, with canopy heights ranging from 20 to 30 meters (Lauriault 1989). These trees have broad-crowns and massive, spreading branches. The bark thickens with age, producing up to 8 centimeter deep furrows into the coarse flat-topped ridges. *P. deltoides* has an extensive range south of the Great Lakes and into central North America but it reaches the northwestern extreme of its range in southern Alberta. In Alberta, *P. deltoides* is found almost exclusively along riverbanks, and may have originated from the Mississippi and Red River basins via the Missouri and Saskatchewan River systems (Brayshaw 1965b). It occurs along prairie rivers with low gradients, sand beds, high suspended sediment loads and freely meandering or braided channels (Bradley 1991). In Alberta its distribution spreads from the Saskatchewan border west along the Red Deer and South Saskatchewan/Oldman rivers to just past Drumheller and Lethbridge, respectively. *P. deltoides* also appears near the Montana border on the Milk River and in isolated pockets on the Bow River below Calgary (Brayshaw 1965b; Rood, personal communication).

Populus balsamifera is also known as the balsam, balm, hamatack, tacamahac, or rough-barked poplar and it belongs to the *Populus* Section *Tacamahaca*. Its specific name *balsamifera* literally means "balsam bearing" in reference to the fragrant, balm-like sap exuded by its buds, and its section name, *Tacamahaca*, originates from the Aztec "tecomahiyac", which refers to a highly resinous tropical plant (Lauriault 1989). The balsam poplar is an intermediate sized cottonwood that can range from 18 to 24 meters in height and 0.3 to 0.6 meters in trunk diameter. Its crown is columnar with an ascending arrangement of branches, and its bark becomes furrowed with age, but not to the extent of that of the prairie cottonwood.

The balsam poplar is very similar in appearance to *Populus trichocarpa*, also known as the black, northern black, western balsam, or Californian poplar. The similarity of these two species has inspired a series of inquiries which have repeatedly grouped and separated their classifications (Brayshaw 1965a). The black cottonwood can reach heights of 18 to 40 meters and trunk diameters of 30 to 150 centimeters (Lauriault 1989).

Balsam poplars tend to occur along foothill rivers with steep gradients, coarse beds, low suspended sediment loads and braided or straight channels (Bradley 1991). According to early accounts by Brayshaw (1965b), *P. balsamifera* ranges throughout the boreal forest frequently as an upland tree and grows mainly on the riverbanks in southern Alberta while *P. trichocarpa* usually appears along riverbanks and alluvial flats from the montane forest region to the west and south, occurring regularly along rivers south of the Bow River. Accordingly, there is overlap in the ranges of the balsam and black cottonwoods lending to the confusion of their classification. For the purposes of this inquiry, the differentiation of *Populus trichocarpa* from *P. balsamifera* will not be attempted. Instead they will be referred to generically as *P. balsamifera.*

Populus angustifolia is commonly known as the narrowleaf, mountain, willow, willow-leaved, bitter, or yellow cottonwood. The first of these common names is a literal translation of the scientific name since the Latin *angustus* means narrow and *folium* means leaf. Although sometimes confused for a willow because of this leaf shape, *P. angustifolia* belongs to Section *Tacamahaca* with the balsam and black cottonwoods. *P. angustifolia* has a smaller stature, only reaching heights of 10 to 15 meters and trunk diameters of 20 to 30 centimeters (Lauriault 1989). It is a common poplar in the Rocky Mountains of the United States but is rare in Canada where the northern tip of its range barely crosses the international border into southern Alberta. Its range extends only as far northeast as Lethbridge (Brayshaw 1965b), and it rarely occurs in pure stands, often becoming lost in the swarm of hybrids that result. The smaller size of *P. angustifolia* in its pure form, often relegates it to being dominated by an overstory of the taller species.

The fifth poplar species in Alberta is the aspen *Populus tremuloides*, more commonly known as smooth-bark poplar, popple, aspen poplar, and trembling, quaking, American, small toothed, or golden aspen. As suggested by its variety of names, *P. tremuloides* has one of the widest distributions of trees in North America. This aspen is an important tree species in the aspen parkland and boreal forests but is uncommon in the prairie riparian zones of Southern Alberta. It can reach heights of 12 to 20 meters and diameters of 0.3 to 0.6 meters (Lauriault 1989). The trembling aspen regenerates almost exclusively clonally by producing extensive stands of suckers from its roots (Barnes 1966), providing an interesting comparison to cottonwood reproductive strategies.

1.1.2 The hybrid swarm in southern Alberta:

The overlap in *Populus* ranges and the propensity of poplars for generating hybrids (Brayshaw 1965b), has facilitated the formation of a unique tri-specific hybrid swarm in the Southern Alberta region. The continuous complex of crosses and backcrosses make it impractical to name each hybrid. However, designations for elementary hybrids occasionally appear in the literature. The hybrid of *Populus deltoides* and *P. balsamifera* has been named *P. x jackii*, and that of *P. deltoides* and *P. angustifolia* is *P. x acuminata*. Since *P. balsamifera* and *P. angustifolia* are both from *Populus* Section *Tacamahaca*, continuous variation is known to occur between them and no specific hybrid designation has been made. For clarity and convenience, the hybrids under consideration here will be presented simply as hybrids, and where necessary or possible, will be defined by their hypothesized parental contributors.

1.1.3 Importance of the cottonwood forest:

Since the riparian woodland represents the only native forest present on the prairies of southern Alberta, a diverse assemblage of other organisms are dependent upon them. The trees, in effect, create a microclimate without which the rest of the riparian habitat would disintegrate. Riparian cottonwoods function in river bank stabilization as their roots can slow or redirect the forces of erosion. Given the stabilized bank and developing soil structure, a host of other vegetation is able to become established. Further, as the forest ages, the cottonwood trees continue to decide the nature of the ecosystem because their sheltering canopy drives a succession of vegetation and attracts an abundance of animal species. Many researchers have found these forests to be vital to prairie wildlife and even essential to certain riparian species (Bottorff 1974, Crouch 1979, and Hubbard 1977). Over 40 mammal, six amphibian and four reptile species are known to inhabit or frequent the riparian cottonwood forests in the Southern Alberta region (Rhodes 1991). Some of the highest breeding bird densities are found in riparian habitats. In Dinosaur Provincial Park, Alberta, along the Red Deer River, Savoy (1991) found that 75% of the breeding bird species bred exclusively in the riparian zone. The cottonwood community is also important to aquatic wildlife, its shade prevents high water temperatures lethal to fish, the root systems reduce silt production that can muddy the water, and fallen debris provides cover for fish and habitat for the invertebrates on which they feed (Rinne 1993 and 1995).

The earliest human inhabitants of this area recognized the importance of riparian woodlands in supplying their most basic needs. Plentiful sources of water, food and shelter encouraged them to camp nearby. The success of such settlements is reflected in the fact that today, three major Indian Reserves in

Southern Alberta; the Blackfoot, Blood and Peigan, are located along river valleys dominated by stands of riparian cottonwoods. The majority of modern settlements have been preferentially placed in or near riparian zones. This decision is primarily based on ready access to water, but added benefits encompass aesthetics, recreation, and the economics involving ranching, farming, mining, and sometimes logging. The riparian zone and associated woodlands are desirable for so many natural and human activities that conflict seems inevitable.

1.1.4 Present condition:

Declining forests:

Presently concern is mounting because riparian cottonwood forests have been found to be declining steadily. Numerous publications have documented decline in these forests across the continent; these include, but are not restricted to, rivers in New Mexico, Montana, Alberta, Colorado, Wyoming, California, and Arizona (Howe and Knopf 1991, Hansen 1989, Rood and Heinze-Milne 1989, Sedgwick and Knopf 1989, Akashi 1988, Buer et al. 1988, Brown et al. 1977). Since cottonwoods are the foundation for the whole riparian ecosystem, their decline signals that the entire system is in danger. The Prairie Conservation Action Plan (1989-1994) was developed by the World Wildlife Fund of Canada to promote the conservation of the biological diversity of Canadian prairies and parklands, and it has recognized these riparian areas as particularly threatened.

Causes of forest decline:

Cottonwood decline may be due to natural or human factors. Natural factors that have always limited the establishment and survival of cottonwood groves include fire, river meandering, drought, flood, beaver activity, and old age. These are ongoing natural processes that tend to occur at a slow enough rate for regeneration to keep pace. Alternatively, human impacts are often prolonged and more severe, leaving lasting gaps in the riparian zone or altering the conditions underlying the system's basic functioning. In Alberta, altered river flows, cattle grazing, clearing for floodplain developments, fire, and beaver activity have been identified as the most significant factors influencing the degradation of riparian cottonwood habitat (World Wildlife Fund Canada and Forestry, Lands & Wildlife, Fish & Wildlife Division 1992). The direct destruction of cottonwoods can be less damaging than activities that alter the system's functioning. The most undermining of such impacts involves the manipulation of the water supply. By their nature, riparian ecosystems are adapted to and dependent on the timing and natural flow of water resources. If the flow is limited and its timing is altered, cottonwood ecology will no longer be coordinated with the water resources, leading to a stressed population and inadequate regeneration. The Prairie Conservation Plan (1989-1994) states that riparian habitats in the prairies are among the most threatened ecosystems primarily due to water and land mismanagement practices (World Wildlife Fund Canada and Forestry, Lands & Wildlife, Fish & Wildlife Division 1992).

Management strategies:

To reverse cottonwood forest decline, the preservation of mature trees is not a complete solution. It would result in an aging forest structure, lacking productivity and variety, with no young trees as replacements. Instead, the preservation of mature trees intact with their community and natural processes is the only way to ensure continued, natural cottonwood survival and reproduction. To enable this, research must detail cottonwood replenishment strategies and survival requirements. Conservation movements undertaken by the World Wildlife Fund of Canada and the Alberta Department of Forestry recognize that more information is needed on methods of (sexual and asexual) reproduction predominating for the three poplar species and their hybrids and on the conditions favouring establishment of young poplars and survival of older trees along different river types (World Wildlife Fund Canada and Forestry, Lands & Wildlife, Fish & Wildlife Division 1992). It is the goal of this project to illuminate the role that asexual reproduction has played in cottonwood regeneration.

1.2 Overview of related research:

1.2.1 Cottonwood Reproduction:

Reproductive strategies:

Flowering plants reproduce sexually by means of seeds or asexually through vegetative or clonal propagation. Cottonwoods utilize a combination of both strategies. The two forms of reproduction differ in adaptive value, and so may be favored differently under different circumstances (Table 1-1).

Given a changing environment where new areas are continually colonizable, seedling-oriented reproduction confers an adaptive advantage. This advantage stems from the dispersive and adaptive abilities of seed-based reproduction. Small seeds are easily dispersed and each requires minute parental investment. As a result, they can be produced in large numbers for dispersal over large areas. Since every seed is the product of a unique segregation and recombination event, each is genetically unique. By dispersing large numbers of unique seeds, the chances are improved that some will land in hospitable environments, and of the new seedlings, a few may be better adapted to the environment than the parent was. However,

Table 1-1. A comparison of the sexual (seedling) versus asexual (clonal) reproductive strategies in cottonwoods. A (+) identifies an advantageous characteristic of the strategy under consideration, and (-) signifies a disadvantage.

	REPRODUCTIVE STRATEGY:	
	Seedling:	Clone:
dispersion:	(+) high	(-) low
introduce genetic variability:	(+) high	(-) low
parental investment:	(+) low	(-) high
survival rate:	(-) low	(+) high
time to mature:	(-) long	(+) short
competitive ability:	(-) low	(+) high

since the dispersive ability of seeds is accomplished by their small size and large numbers, each embryo has only limited nutrients to supply it to the point of self-sufficiency. For this reason, seedlings are initially vulnerable to environmental factors, and are less competitive than established vegetation. For successful establishment, a seed generally requires dispersal to an open area with sufficient moisture. Given the number of seeds released by the parent, relatively few arrive in hospitable sites, and of those, even fewer survive to maturity. Although seedling-based reproduction is a risky endeavor, in a dynamic environment with colonizable spaces, seedling-based reproduction has advantages that can compensate for the disadvantages. Consequently, the sexual component of cottonwood reproduction is adapted for recruitment in the high-disturbance environments of meandering river floodplains (Bradley and Smith 1986).

In a stable, highly competitive environment, clonal reproduction can confer an adaptive advantage. In such a situation, producing genetically diverse offspring may be less important, or even unfavorable since the action would reshuffle an already well-adapted genome. Instead, the progeny of vegetative propagation are genetically identical to the parent, and similarly adapted to that constant environment. In return for higher, prolonged parental investment, ramets are more vigorous and competitive, and so their survival rates surpass those of seedlings. The reduced dispersive ability of clones should be less problematic in stable, highly competitive environments where newly colonizable areas are rare.

The riparian environment demonstrates an interesting polarity of conditions. It is characterized by alternating periods of change and stability. The environment is dynamic on the one extreme, because as a river meanders across the wide valley floor, it erodes old banks and deposits new point bars. When late spring finds these moist floodplains newly deposited and scoured of vegetation by the movements of ice, there can be a rich opportunity for cottonwood seedling establishment. However, the specific flood conditions required for successful cottonwood recruitment are irregular or infrequent (Barnes 1985, Mahoney and Rood 1990), so that periods of years or even decades may pass before conditions become conducive for successful seedling recruitment (Bradley and Smith 1986, Johnson 1994, Stromberg et al. 1993).

Alternately, other areas of the same environment are more stable and competitive. Within established cottonwood stands there is very little space that has not already been colonized by the trees or their associated understory. Unless disturbed by the meandering river or other factors, these stands can reach considerable age and relative stability, making it nearly impossible for a poorly competitive cottonwood seedling to establish under such a canopy. However, a clonal shoot linked to an established root system would have a much higher chance for success.

In response to the polarity of the riparian condition, it is possible that cottonwoods utilize both reproductive strategies in response to their environment. With seeds to facilitate dispersal and genetic variability, and ramets to provide stable replenishment within a grove, the cottonwood would be assured of productivity even in years where conditions prohibit seedling-mediated reproduction. In a predominantly arid climate this ability would have significant adaptive value.

Although the trends exist, sexual and asexual strategies are not exclusive to dynamic and stable environments respectively. In particular, clonal revegetation is commonly promoted by flood-related disturbance to riparian habitats (Gecy 1990). The critical requirement of cottonwood seedlings for full exposure to sunlight makes them poor competitors in vegetated sites (Fenner et al. 1984), and so does not permit them the same flexibility of environment as compared with clones.

Seedling-based reproduction in cottonwoods:

Discussions of cottonwood reproduction are often biased towards sexual reproduction. Common knowledge suggests that reproduction in plants revolves around seed production. Indeed, cottonwoods produce and release viable seeds on a grand scale; a single mature riparian cottonwood can produce tens of millions of tiny seeds annually (Bessey 1904), each of which is equipped with a pappus of fine threads which assists dispersal by wind or water. Since each seed is only about one millimeter in length, the enclosed nutrient supply is limited and the seed's viability lasts only days (Engstrom

1948) or weeks (Moss 1938). For success in this narrow window of time, the seed must germinate on a moist site at a time when the river is receding (Mahoney and Rood 1991, 1993). Natural river stages follow partially predictable periods of seasonal flood and decline, and cottonwood seed release is timed to coincide with the period of highest water levels in the late spring (Bradley et al. 1991).

The vast majority of seedlings fail to survive because their moisture requirements are not met (Mahoney and Rood 1990). Survival of seedlings can be further limited by flooding or ice scouring in the following years (McBride and Strahan 1984). Thus surviving seedlings usually form narrow arcuate bands paralleling the river, at elevations low enough to access the water table, yet high enough to escape flood and ice scour. The age structure of *P. deltoides* stands found on the Milk River by Bradley and Smith (1986) indicated that 75% of those trees originated from flood events with flow-magnitudes greater than a one in ten year event. Considering such trends, the opportunity for successful seedling establishment is severely limited, and it is thought that in most years no seedlings survive at most sites (Mahoney and Rood 1990, Virginillo et al. 1991). Thus, despite enormous sexual reproductive potential, seedling success is minimal in most years.

Clone-based reproduction in cottonwoods:

Asexual reproductive mechanisms involve cloning events that produce genetically identical ramets. Investigations into poplar reproduction often fail to address contributions made by asexual recruitment. The most recognized modes of clonal reproduction in poplars are root-suckering, the production of new shoots from existing roots, and shoot-suckering, the production of new shoots from existing, buried shoots. Since suckers are initially supported by the parental root system, their success is less limited by environmental constraints than that of seedlings. In this way, asexual forest rejuvenation can occur even during intervals of years or decades where conditions are unfavorable for seedling establishment. Given the proper conditions, branch fragments can also root (Galloway and Worrall 1979, Reid et al. 1992, and Zasada et al. 1981), contributing in a less recognized way to asexual recruitment.

Very few studies have been devoted purely to investigating cottonwood clonal processes. A review of publications which report asexual mechanisms in the three species of interest; *P. deltoides*, *P. angustifolia*, and *P. balsamifera*, and in one additional species from each *Populus* section; *P. fremontii* from section *Aigeiros* and *P. trichocarpa* from section *Tacamahaca*, is presented in Table 1-2. The vast majority of these reports only briefly mention clonal characteristics.

Distinguishing clones from seedlings is problematic. Even while young, suckers can be mistaken as seedlings because as well as occurring among mature trees, they can also establish in floodplain zones more commonly associated with seedling recruitment. "Flood-training" (Everitt 1968), involves shoot-suckering along the length of flood-felled trunks which are oriented by the direction of river flow. The series of shoots produced parallels, and so resembles, the classic arcuate-banded arrangement of seedlings, especially if the original trunk is degraded or buried by sediment over time.

Table 1-2. Review of publications reporting cottonwood asexual reproduction. Studies with a primary focus on asexual mechanisms are flagged with one or two asterisks; two for the highest degree of relevance.

a) Section *Aigeiros*:

	Maini 1967	-stem cuttings root with relative ease
	Braatne et al. 1996 (in press)	-only shoot-suckers, especially from flood-training
	P. deltoides:	
	Fuller 1912	-dependent on vegetative reproduction for maintenance
	Read 1958	-excellent ability to produce shoot and root-suckers -lesser ability in older trees
	Maini 1967	-do not root-sucker as readily as other poplars
	Everitt 1968	-flood-training of saplings -suckering was rare and only observed in old, thin forests -young trees among older ones were often suckers
	Wilson 1970	-all saplings were thought to be from vegetative processes
	Hall 1973	-flood-training and shoot-suckering occurs, but is uncommon in mature trees
	Schier & Campbell 1976	-naturally root-suckers -root cuttings suckered (proximal shoots and distal roots)
	Zsuffa 1976	-rooting of stem cuttings (not as well as in *Tacamahaca* species) -shoot-suckering occurs from stumps, root-suckering is uncommon
*	**Bradley 1982**	-shoot-suckering in response to beaver, flood, and fire damage -excavations revealed flood-training in several young trees -sprouted buried branches were observed three times -root-suckering was not observed
	Dickmann & Stuart 1983	-young stumps produce vigorous sprouts
*	**Barnes 1985**	-57% of all cottonwood stems were suckers -shoot and root-suckers are common in the smaller size classes -especially due to repeated beaver browse
	Akashi 1988	-root-suckering after fire and shoot-suckering after beaver -less root and shoot-suckering in older trees
	Bradley et al. 1991	-flood-training of saplings and shoot-suckering from stumps -root-suckering seldom occurs
**	**Rood et al. 1994**	-no root-suckers after extensive excavations of small saplings -shoot suckers proven through excavation
	P. fremontii:	
*	**Irvine & West 1979**	-root-suckers and dense clone groups of mature trees
	Pope et al. 1990	-stem-cuttings rooted, but root-cuttings failed
*	**Howe & Knopf 1991**	-excavation showed trees under 26 years old were root-suckers

b) Section *Tacamahaca*:

Maini 1967	-stem cuttings root with relative ease
Braatne et al. 1996 (in press)	-shoot and root-suckering and branch fragment rooting

P. angustifolia:	
Schier & Campbell 1976	-natural root-suckering and from excised root-fragments
Baker 1990	-existence of many root-suckers
Bradley et al. 1991	-flood-training of saplings -stump shoot-suckering and root-suckering
Rood & Mahoney 1991	-profuse shoot and root-suckering (especially after disturbance)
** Rood et al. 1994	-shoot and root-suckering in small saplings excavated
P. balsamifera:	
Fowells 1965	-shoot and root-suckers, and rooted branch fragments
Maini 1967	-reproduces vegetatively towards northern limits
Hellum 1973	-regeneration in Alberta is commonly by suckering
Schier & Campbell 1976	-occurrence of natural root-suckering -artificially excised root fragments suckered
* Zasada et al. 1981	-clearcut logging and scarification induced root & shoot-suckers -buried shoot fragments rooted
Dickmann & Stuart 1983	-will rapidly invade disturbed wet sites by suckering
* Edwards & Dunwiddie 1985	-suckering can lead to the formation of extensive clones (10 - 50) -small saplings among mature trees were root-suckers -both even-aged and gradually expanding clones were observed
* Comtois et al. 1986	-small stands of one or many clones in eastern North America
Rood & Mahoney 1991	-capable of shoot and root-suckering profusely
** Rood et al. 1994	-shoot and root-suckers in small saplings excavated
P. trichocarpa:	
* Galloway & Worrall 1979	-natural rooting of branch fragments shed via cladoptosis
Dickmann & Stuart 1983	-young stumps produced vigorous sprouts -root-suckering occurs

c) Miscellaneous Observations:

Moss 1938	-Alberta poplars reproduce naturally by root suckers, while seedlings are rare
Maini 1967	-reproduction by root-suckering is common among poplars
Shaw 1976	-the majority of branch fragments on gravel bars had not sprouted even after partial burial
Strahan 1984	-where mechanical abrasion from river flows was severe, asexual reproduction was as common as sexual
Rood & Mahoney 1990	-suckering obscures arcuate banding from seedling reproduction, contributing to forest complexity and maintenance -root grafts may form between neighboring trees -fire, ice-scour, beaver browse promotes root/shoot-suckers -root-suckers due to scarification at edges of gravel pits
Reid et al. 1992	-capable of shoot & root-suckering and branch fragment rooting -flood-training of buried saplings
** Rood et al. 1994	-half of saplings from the early 1990's in S. Alberta were clonal -root sucker occurrence increased with distance from the river -clonal reproduction compensates for irregular seedling recruitment and provides replenishment between flood events

Southern Alberta's native cottonwoods are capable of suckering to varying degrees (Table 1-2). In *P. deltoides*, *P. balsamifera*, and *P. angustifolia*, shoot-suckering has often been linked to the trauma of beaver-browse, flood-training, or fire damage. Root-suckering appears to be more variable among these species, since *P. balsamifera* and *P. angustifolia* have been observed to root-sucker profusely in response to root scarification, while instances of root-suckering in *P. deltoides* are less frequent and less prolific.

The rooting ability of cottonwood shoot cuttings has been well recognized in poplar silviculture. Indeed, the most widely used method for large scale silvicultural propagation of cottonwood is by the rooting of stem cuttings collected in the late winter (Zsuffa 1976). All of the Southern Alberta species can be propagated under controlled conditions from stem cuttings taken after winter dormancy (personal observation). Natural processes of flood and ice-scouring, beaver activity, and wind-pruning can also result in physiologically active branch fragments. In some *Populus* species, a process termed cladoptosis results in the physiological abscission of lateral twigs and branches via a 'ball and socket' abscission zone (Dewit 1992, Galloway and Worrall 1979). These fragments have the potential to root naturally under moist conditions in *P. trichocarpa* (Dickmann 1983, Galloway and Worrall 1979), and in cottonwood species found in southern Alberta (Rood et al. 1994).

Shoot fragments act as propagules analogous to seeds since they have dispersal ability and must be wholly self-sufficient to survive. Identical to seedlings, the establishment of shoot fragments on the floodplain would be strictly limited by their moisture requirements. The rooting of branch fragments is favored by high temperatures (20 to 27 $^{\circ}$C), high moisture availability, and darkness (Zsuffa 1976) that could be produced by fragment burial in newly deposited sediments. Thus, the rooting of branch fragments as a reproductive strategy may be of more importance in wetter times, or regions. There is also species variation in the rooting ability of such fragments as those from *P. deltoides* do not root as easily as those from *Tacamahaca* species (Dewit 1992, Zsuffa 1976). Other factors contributing to differences in fragment rooting ability include the tissue's age and where it was positioned on the parental tree (Zsuffa 1976).

Sexual versus asexual replenishment in cottonwood groves:

To fully understand riparian cottonwood regeneration, the contributions of sexual versus asexual replenishment must be recognized. In 1994, Rood, Hillman, Sanche, and Mahoney systematically excavated 690 cottonwood saplings of the three species and their hybrids, on the floodplains of four rivers in the Oldman River Basin to determine the relative proportions of sexual versus asexual contributions to recruitment. They concluded that 48% of the saplings originated through clonal mechanisms. However, because recruitment of seedlings is known to vary drastically between years, this proportion of clonally originated saplings might not be reflected in the mature cohort. As an extreme example, 1995 flooding on the Oldman River reached the magnitude of a one in one hundred year event, and resulted in record seedling recruitment (Rood pers. comm.). Following such an event, the number of clones would be dwarfed by millions of seedlings. Due to the poor survivorship of seedlings as compared with clones, the proportions of each found at the time of initial recruitment versus that discovered in later years would shift in favor of clones. Rood et al. (1994) recognized these difficulties and called for further investigation into the extent of clonal origin among mature trees. The difficulty of engineering such an inquiry stems from the problem of distinguishing clonally versus sexually originated mature trees. This project will address this problem.

1.2.2 Investigating ramet identity:

Definition of terms:

A definition of terms must precede any discussion of clonality. The concept of cloning is used across disciplines to describe exact replication. Here, a clone will be defined as a group of organisms originating from a single individual by asexual reproduction, so that all members of the group are genetically identical. The entire group is termed a genet, and each progeny clone, a ramet. The generic term "clone" can refer either to the entire genet or to a single ramet, so when the distinction is important, the more specific term, ramet or genet, will be used.

There is some controversy over whether to regard the cloning process in *Populus* as reproduction or regeneration. These terms are often used synonymously, without consideration for their differing implications to population ecology. The distinction in terminology can reflect the physiological autonomy of the individual. A ramet that is or becomes self-sufficient from the parent is considered the result of asexual reproduction. Alternatively, a ramet that continues to be dependent on the parent is essentially part of the same individual and is considered vegetative regeneration. As this convention is adopted for simplicity, it should be remembered that ramets derived from either process still remain genetically equivalent to the parent despite physical separation or lack thereof.

Clonal-connections and excavation studies:

In isolation, there are no defining characteristics that label a mature cottonwood as having arisen from a seedling or a clone. The only way to distinguish such origin is to trace past relation to a parental individual. In the case of seedlings, the parent can be a great or short distance away and will not foster a physical connection to the progeny. Since there will not be vestiges of origin for seedlings, one must assume seedling origin if no evidence of clonality is available. In clones, the parental connection is more direct. Since sucker originated ramets can remain linked to the parent semi-permanently, the existence of root attachments seems to constitute proof of clonal relationship. Unfortunately, this is not the case because over time cottonwood root connections can disintegrate or form between unrelated individuals (Rood and Mahoney 1991). However, since excavations and other methods for tracing root connections are intuitive and provide the most direct answer, they have often been utilized in initial attempts at clone delineation. For example, the aspens are more consistently clonal members of the *Salicaceae* family, and success in tracing root connectivity has been demonstrated for their clones (DeByle 1964, Tew et al. 1969).

Isolated instances of excavation have been reported for cottonwoods (Shaw 1976, Bradley 1982, Rood and Mahoney 1990, and Howe and Knopf 1991), but few complete excavation surveys have been attempted because they demand intense investment of time and labour, are highly destructive, and still need to address the potential for root-connection and root grafting over time. The method is more suitable for investigating immature saplings, as Rood et al. (1994) systematically excavated cottonwood saplings on floodplains and so discovered substantial asexual recruitment. Since physical connections in mature cottonwoods are undependable indications of clonal relationship, a less direct method of tracing relationship to parental trees must be found.

Methods for distinguishing clones from seedlings:

A ramet is genetically identical to the other members of its genet, so if two or more individuals are genetically identical, it follows that they must be clonally related. Methods of genetic, biochemical, morphological, and phenological comparison are available to analyze genetic similarities. None of these methods can prove two genomes to be exactly identical and thus clonally derived, but by detecting differences in genetically conserved characters, it is possible to exclude dissimilar members from a proposed genet. After such attempts at division, the likelihood that an intact group represents a clone depends on the stringency of the determination of dissimilarity.

-biochemical & genetic methods:

Biochemical markers have been used in poplar research to clarify species relationships. They improve powers of clonal delineation since errors due to environmental influence and subjectivity in the interpretation of physical traits are prevented. Biochemical markers familiar to poplar research commonly employ isozymes, more specifically allozymes (Rajora 1988, Rajora 1989, Rajora and Zsuffa 1989, Rajora and Zsuffa 1991, Rajora et al. 1991). Aspen clone groupings have also been constructed using electrophoresis of isozymes by Cheliak and Pitel (1984).

Genetic research in poplars has utilized restriction fragment length polymorphisms (RFLPs) in DNA (Keim et al. 1989), ribosomal DNA (rDNA) (D'Ovidio et al. 1991, D'Ovidio 1992, Faivre-Rampant et al. 1992, and Faivre-Rampant and Jeandroz 1992), mitochondrial DNA (mtDNA) (Barrett et al. 1993), and chloroplast DNA (cpDNA) (Rajora and Dancik 1995a, 1995b, and 1995c). There are disadvantages to the use of RFLPs since they are time consuming, expensive, and limited by restriction enzyme number

(Castiglione et al. 1993) or to species which have their genetic maps constructed (Faivre-Rampant et al. 1992).

Methods allowing direct genomic comparison of potential clones have advantages related to reduced risk of influence by environmental factors. Since an individual's genotype is strictly conserved, and members of a genet should be exact duplicates of one another, genetic differences between them should be limited to individual somaclonal variation or mutation. Various genetic methods are now available to the clonal researcher for building such analyses.

Since it would be impractical to sequence the entire genome of an organism to compare it gene by gene to that of a potential clone, a better approach would involve DNA fingerprinting. The method uses the polymerase chain reaction (PCR), an enzyme-based procedure for amplifying DNA sequences specified by primers. The products of the PCR reaction are separated and visualized via gel electrophoresis. A lane containing a series of bands will result, with each band representing a specific DNA fragment. In this way the banding patterns of different individuals can be compared. By properly selecting the primers and monitoring the degree of polymorphism within the DNA, the banding patterns produced can be individual-specific and so should be able to indicate differences between unrelated individuals. The arbitrarily primed polymerase chain reaction (AP-PCR) (Welsh and McClelland 1990) and random amplified polymorphic DNA (RAPD) (Williams et al. 1990) are based on these principles, and would be likely choices for this application. These methods are relatively simple, fast, inexpensive, and require little knowledge of the genetics or biochemistry of the species being studied. Aspen researchers have already explored the use of these techniques in pursuit of accurate clone delineation. Rogstad et al. (1991)

used the M13 repeat probe for separating aspen clones. Several attempts at clonal delineation in *Populus* have been made using RAPD technology. Castiglione et al. (1993) used RAPD fingerprinting to discriminate among 32 clones taken from 13 cultivated species of the genus *Populus*. Among the clones tested were 3 from *P. deltoides* and 18 from *P. x euramericana* (a hybrid of *P. deltoides* and *P. nigra*). The RAPD approach grouped them into the proper species categories and was able to distinguish between them. Lin et al. (1994) also used RAPD fingerprinting for differentiation of poplar and willow clones. They differentiated 15 poplar and 15 willow clones by using 4 random DNA primers and the M13 universal primer.

-morphological & phenological methods:

The use of morphology as a classification tool dates back to the very first attempts at taxonomy. Today, phenotype is still applied to the study of systematics, although there are differences of opinion over whether phenotypic characters and molecular ones are equally useful. Each approach has strengths and weaknesses depending upon the circumstances of the application. The 'magnifying glass' of phenotypic observation can be compared to the 'electron microscope' of genetic analysis. While very different, they are related enough to invite competition. Neither is incorrect, but each has distinctions for proper use. When used appropriately, both should be extremely useful and highly complimentary.

Morphological and phenological comparisons can be applied to the analysis of genomic similarities between potential clones. Although indirect, these approaches do offer advantages related to their ease of observation and long history of use. Since members of a genet share a genotype, they will also share any heritable phenotypic characteristics of morphology (physical form and structure) and phenology (timing of processes). Since phenotype is the result of the interaction of genotype with the environment, the usefulness of such characters in clone delineation depends on their environmental insensitivity and degree of variability. Ideal characters for the study of clones would provide enough variability to distinguish individuals from the rest of the population but not so much that variability would appear within one individual. The chosen characters would need to be priorized according to their type of variability, with characters most directly linked to the genotype incorporated into the analysis first for maximum influence. With the addition of characters into the analysis, the body of potential clones would be sequentially subdivided according to dissimilarity, and clone groups would emerge.

To evaluate the utility of phenotype in distinguishing cottonwood clones, it is useful to first review examples from aspen research. Clone delineation in aspen species has often involved the use of morphology and phenology. In some of the most complete studies of their kind, Barnes (1959 and 1969) was able to distinguish clones in trembling and big tooth aspen based on select phenotypic characters (Table 1-3) and geographic proximities. Related types of observations have been used by Blake (1964), Kemperman (1977) and Andrejak (1969) for clone identification. Following the example of these aspen studies, a list of similar characters are available for clone research in cottonwoods (Table 1-4). By repeatedly dividing a population of cottonwoods according to dissimilarity of these characteristics, clone groups should emerge if they do exist.

Table 1-3. (reproduction of Table 6 from Barnes 1969) Characteristics useful in the field identification of aspen clones, ranked by season and listed in descending order of usefulness.

A. Spring
    1. Sex
    2. Time of flowering and floral characteristics
    3. Time, color, and progression of leaf flushing
B. Autumn
    4. Leaf coloration
    5. Time and progression of leaf fall
C. Summer
  Leaf Characteristics
    6. Leaf shape, color, and size
    7. Configuration of blade base
    8. Leaf margin: tooth number, size, and shape
    9. Configuration of blade tip
D. All Seasons
  Bark characteristics
    10. Bark texture
    11. Bark color
  Stem characteristics
    12. Stem form
    13. Branching habit (branch angle & length, internode length)
    14. Susceptibility to injury
      a. Sun scald
      b. Frost crack
      c. Insect and disease injury
    15. Miscellaneous characteristics
      a. Pruning ability
      b. Leaf rust
      c. Aphid galls
    16. Vertical profile

Table 1-4. Characteristics useful in the field identification of cottonwood clones, ranked by season and listed in descending order of usefulness.

A. <u>Spring</u>
    1. Sex
    2. Timing of flowering
    3. Timing and progression of leaf flushing
B. <u>Autumn</u>
    4. Timing of leaf color change (senescence)
    5. Time and progression of leaf fall
C. <u>Summer</u>
  Leaf Characteristics
    6. Leaf shape (species/hybrid identity)
    7. Leaf measurements:
      -blade length
      -petiole length
      -blade width
      -tooth depth
      -petiole to blade angle
D. <u>All Seasons</u>
  Stem characteristics
    8. Stem form
    9. Branching habit
    10. Susceptibility to insect or disease injury

2.0 THE "PROBLEM"

2.1 Theoretical Framework of the Study:

A rigid framework of hypotheses guides this investigation of clonal cottonwood regeneration. Based on the premise that the most reliable way to trace asexual origin in mature cottonwoods is to discover spatially grouped clones that share heritable characteristics and so indicate a shared genome, there are three successive levels of inquiry. The first asks if there is evidence in mature cottonwood forests that asexual recruitment has occurred. If this evidence exists, the next level asks if it is possible to detect and define groups of potentially clonally-related mature cottonwoods according to phenology and spatial characteristics. After successful grouping, the final level asks how abundant clonally originated cottonwoods in mature groves are, and if differences exist in their patterns of clonality.

2.1.1 Is there evidence in mature cottonwood forests of asexual recruitment?

Is there evidence that asexual recruitment has occurred? According to the premise that clonal regeneration tends to produce groupings of identical individuals, the key to finding evidence of asexual recruitment lies in determining the spatial distribution of heritable phenotypes. Thus, the first hypothesis to be tested expects a random distribution of phenotypes. A non-random spatial distribution in the mature population may be the result of one or more of three conditions. Firstly, environmental variation may be responsible if a particular phenotype conferred survival advantage at a particular location, and caused a cluster of similar individuals to establish there. To minimize the risk of this effect, a stable, uniform study site must be chosen to reduce the influence of environmental variation. The second explanation for non-random distribution of mature phenotypes claims that if seed dispersal is non-random, and siblings show a high degree of similarity in the traits under investigation, a patterned spatial distribution could result. The dispersal of cottonwood seeds is thought to be randomized somewhat due to wind-mediation, but the potential for similarity among sibling seedlings should be investigated. The third alternative is that cottonwood reproduction has an asexual element where the production of proximal, identical ramets results in a non-random spatial distribution of phenotypes. After eliminating the first two alternatives, it can be concluded that there is evidence of asexual recruitment.

2.1.2 Delineating mature clones using phenotype and proximity?

Once it has been established that the patterns observed in the distribution of mature cottonwoods are due to asexual regeneration, the second stage of inquiry asks whether it is possible to hypothesize groupings of these clonally-related mature cottonwoods according to phenotypic and spatial characteristics. The population should be surveyed for a series of select, environmentally-insensitive phenotypic characters. After careful consideration it should be possible to divide the cottonwood population into similarity-based groupings. The more similar and proximal members of a group are, the more confidently they will be deemed clonally-related. For this reason there will be a different level of confidence for each grouping, and the researcher must decide the level at which differences in phenotype become significant enough to indicate individuality versus clonality.

2.1.3 Trends in clonal nature and implications for cottonwood regeneration:

After the grouping of clonally related trees is completed, the third and final level of inquiry concludes the investigation by asking for a description of the clones discovered and the implications to cottonwood regeneration.

These results will provide new perspective to viewing cottonwood population structure. Especially interesting insight will be found regarding the general proportions of cottonwoods with clonal relationships, the numbers of individual genotypes as compared with the number of individual trunks; and the clonal tendencies of the different species and the sexes. Depending on how representative the study site was, inferences may be made to other similar riparian cottonwood forests across southern Alberta.

2.2 Research Design:

2.2.1 Study site selection:

A study population with minimal environmental variation was required to ensure that the variation observed in traits within the population had genetic rather than environmental causation. Although it is impossible to guarantee that a homogeneous environment has always prevailed at a given site, there are ways to minimize the chance of encountering a history of variation. Range in elevational profile, site size, and degree of human influence were factored into the decision.

Elevational profile provides useful insight into the history of a riparian zone. In general, gradations in elevation reflect years of river movement. Rivers in southern Alberta swell each spring with the runoff of snow melt from the mountains. Depending on the intensity of these floods, the increased flow powers the movement of sediment, eroding old banks and depositing new floodplains. In this way, the highest elevations represent the oldest sediments undisturbed by river flow, and lower elevations have more recent histories of disturbance. According to this cycle, the more even the elevational profile is across a site, the more likely its history is to have involved consistent environmental conditions. Thus one way to minimize within site variation is to choose one with an even elevational profile. For an added measure of stability, the elevation of the study site should also be high enough to preclude regular influence by flood modification.

The size of an area affects its potential for variation. Minimizing the size of the site will thus reduce this potential. Since repeated censusing of all individuals is required, site size must also be restricted for the practical reason of managing the sample size. The final criterion requires that the site be reasonably free from variation caused by human activities while still being reasonably accessible for repeated sampling.

2.2.2 Census of phenotype:

To evaluate the spatial distribution of phenotypes within the study population, measures of structural similarity (morphology), functional similarity (phenology), and spatial context were to be surveyed for every individual. The selection of characteristics were chosen according to their ability to reflect the genotype, and so diagnose clonal relationships. These characteristics are listed in Table 1-4, and will be described in detail.

A cottonwood is either male or female for its entire lifetime as a direct consequence of its genotype. Sex determination can only be accomplished using flowering characteristics which are observable briefly in the early spring. Since immature trees do not flower, it is not possible to determine their sexes. In both sexes, the flowers are grouped into inflorescences which are termed catkins. The sex of a cottonwood can be diagnosed by the color of its catkins; the male catkins are colored brilliant red from their anthers, while the female catkins remain pale green. The other developmental stages that can serve to differentiate male from female catkins as they mature are depicted in Fig. 2-1 and Fig. 2-2. After repeated observations of flowering phenology, the confidence in the determination of tree sex is strong.

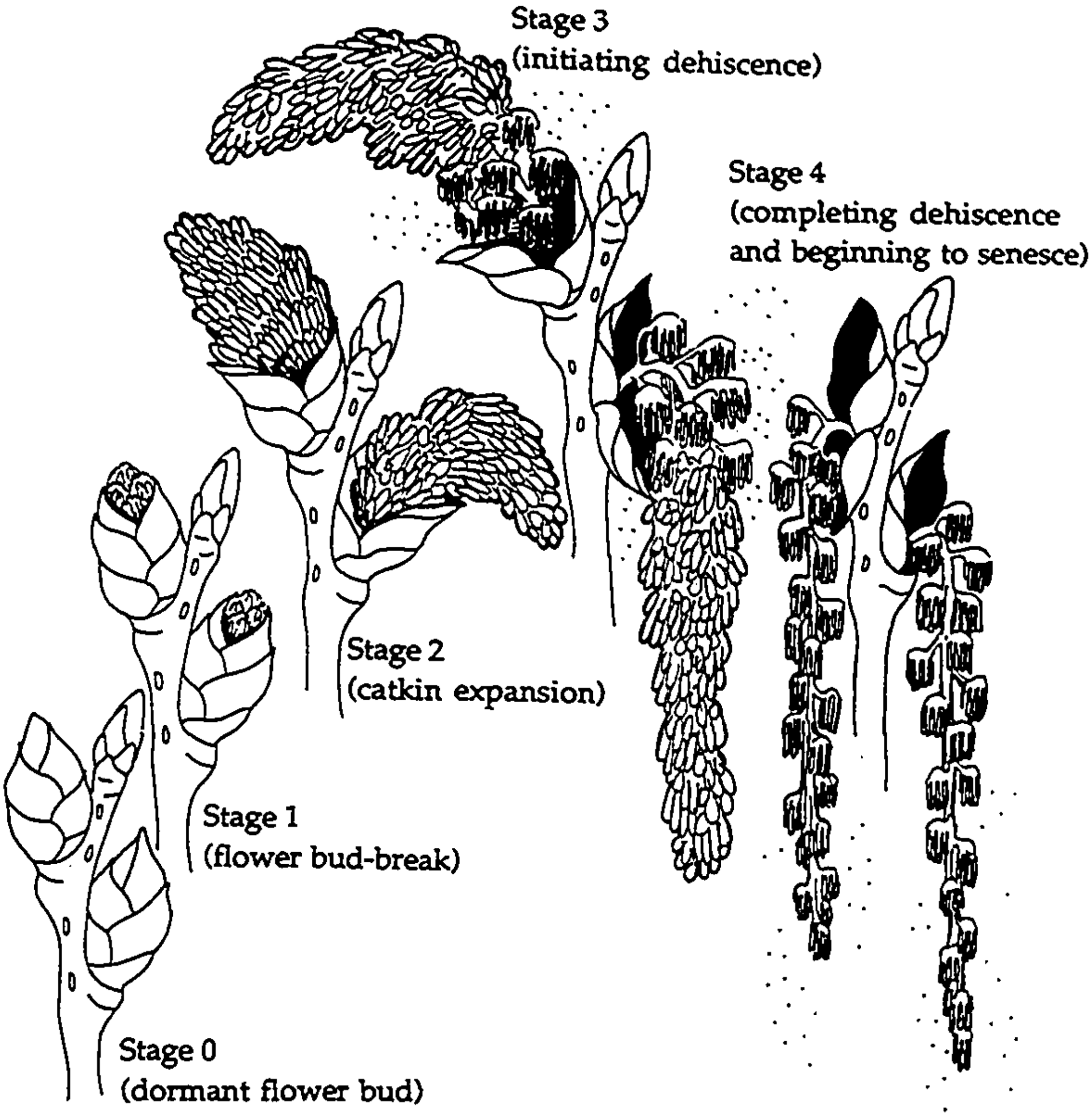


Figure 2-1. The five flowering stages in male cottonwoods.

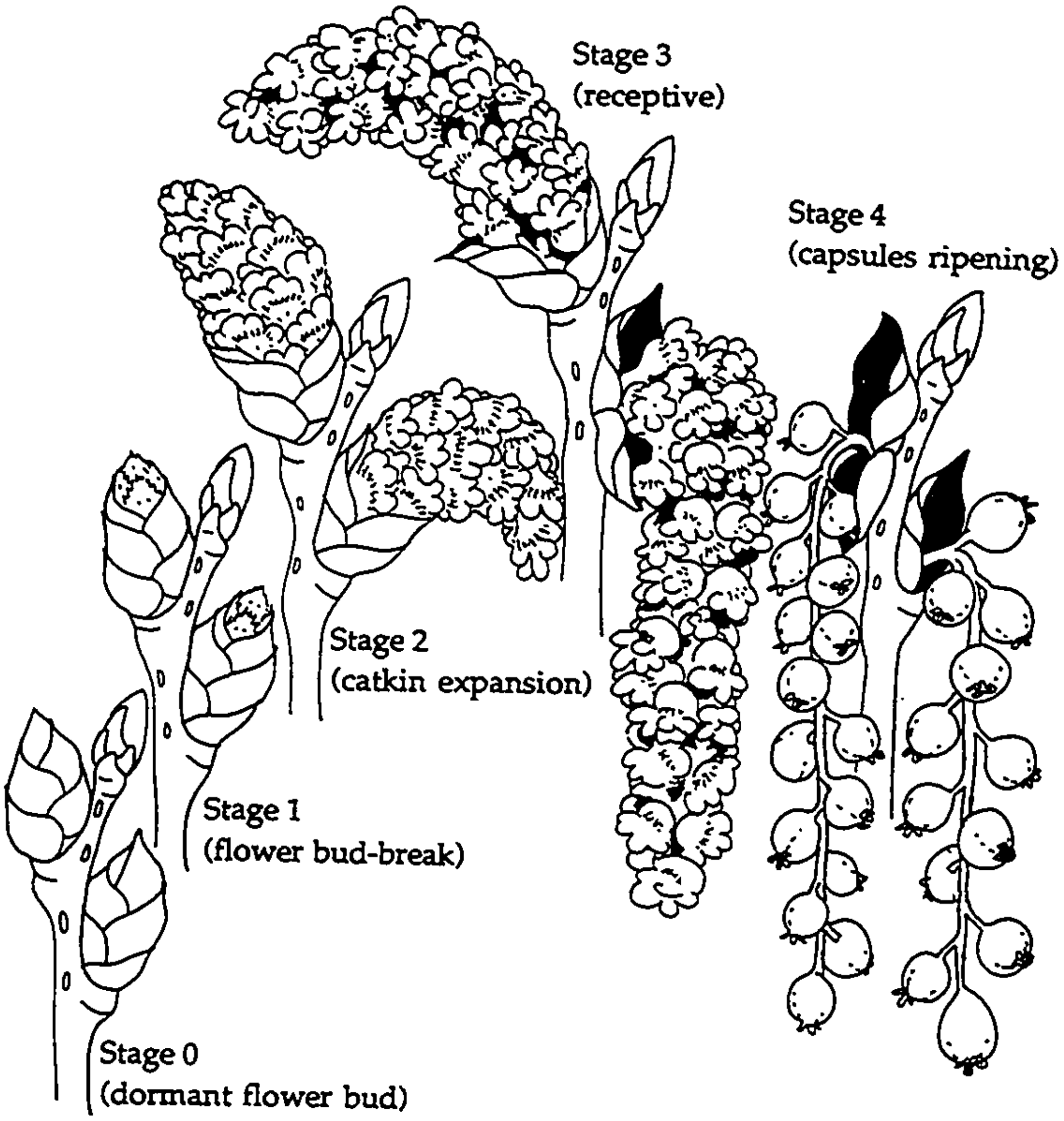


Figure 2-2. The five flowering stages in female cottonwoods.

Species composition is the next most heritable characteristic. Since there are at least three interbreeding species, a wide range of hybrid combinations can occur. Hybrid composition can be classified according to leaf shape (Brayshaw 1965b, Eckenwalder 1984, and Rood et al. 1986). Additionally, measurements of leaf dimensions can detect more subtle differences useful in differentiating clones of the same general species composition.

Stem form and branching habit can be incorporated into a general classification of trunk architecture. This trait is difficult to quantify, is likely related to species identity, and is probably complicated by age and health-related effects. Thus, the usefulness of trunk architecture is limited, and might only serve to support species identification.

Susceptibility to insect or disease injury is tied, through physiology, to the genome. The new shoots of native riparian poplars in southern Alberta are naturally infected by the poplar bud gall mite, *Aceria parapopuli* (Keifer) which stimulates the formation of cauliform-shaped galls. Although these galls may be found on most poplars, some of the hybrids are thought to be especially susceptible (Rose and Lindquist 1982). If susceptibility is influenced by species composition it may also be revealed at an individual level. With uniform mite-exposure across a site, genetically susceptible trees should be apparent by the higher numbers of galls they host. Clonally related individuals would be expected to share the same heritable susceptibility to gall infestation. Mite galls accumulate over periods of years, so the potential influence of tree age and size must also be recognized.

The phenological characteristics of interest involve the timing and duration of flowering, and that of leaf flushing, senescence, and drop. These cottonwoods are specifically adapted to the riparian conditions of southern Alberta. For this reason they coordinate their phenology to capitalize on the annual cycles of water and temperature, and to synchronize with members of the opposite sex, to ensure both survival and contribution to sexual reproduction. Because of the importance of such timing, it is likely under strong genetic control, and thus appropriate for use in clonal discrimination. The timing and duration of such phenological events must be observed over periods of days or weeks, so a complete census must be collected on each of a series of observation dates.

To incorporate a spatial context into the analysis, the distances between trees and the relative locations within the site are required. Following the mapping of all individuals within the site, a set of X - Y coordinates can be assigned to each tree and used for calculating distances between trunks or for locating any trunk within the study site.

Additional observations can be made to provide a general impression of forest structure. An obvious example is trunk circumference taken at breast height. Although it cannot accurately depict tree age in cottonwoods (Everitt 1968, Mahoney and Koegler 1990), it does provide a simplistic index of tree size and maturity. Another occasional observation involves connectivity between adjacent trunks. Physical association of this type, although it does not constitute proof, can be due to clonal relatedness. Miscellaneous observations, such as those pertaining to tree health, can explain anomalies and avoid error where the expression of characters result from factors beyond the influence of genotype.

2.2.3 Analysis of similarity among siblings:

Cottonwoods are wind pollinated; the male cottonwood flowers release enormous numbers of minute pollen grains to be delivered to receptive female flowers by the wind. As each seed develops, it is equipped with fine cottony threads; the pappus, to aid in its wind or water-mediated dispersal. Following from the expectation that wind scatters both pollen and seeds randomly, the chance of a pair of full-siblings landing adjacently on a suitable site, and surviving to maturity is infinitely small. Further, to have three or more full siblings establish in such a way becomes increasingly unlikely. Given the odds of such an event occurring, it would not be expected to occur consistently enough to be the cause of widespread patterning.

To prevent mistaking phenotypically similar siblings for clones, it would be useful to understand the potential for phenotypic similarity among siblings. Sibling seedlings can be grown under controlled conditions for the analysis of this phenotypic variability. For such greenhouse trials, full-siblings from parents of the same species should have the highest degree of genetic similarity of any non-clonally related individuals. However, due to the presence of at least three interbreeding species and their hybrids, only a minor occurrence of such simple crosses would be expected naturally.

To produce full-sibling seedling groups, controlled crosses must be imposed to ensure that only a single male contributes to pollination. A simpler alternative is to raise seedling groups with half-sibling relatedness. By collecting ripe catkins just prior to seed release, one can be confident of common maternal contribution. Poplar seedlings are fast growing under optimal conditions and are capable of providing enough leaves within a few months to allow leaf shape comparisons. Unfortunately, it would take many years in a plantation-setting before the sex and phenology of such trees could be analyzed.

2.2.4 Generating clone-groupings:

Using the morphological and phenological characters, the population can be repeatedly divided according to degrees of dissimilarity to eventually arrive at hypothetical clone groupings. The first partition should be made according to sex, since this character is discrete and highly heritable. Since the sex of non-flowering individuals cannot be known, these individuals should be included in both the male and female categories. The next divisions should reflect differences in species. Due to the hybridizing nature of the population, the three species do not form discrete groups. Instead, the hybrids exhibit continuous variation in their species-related characteristics. This is especially true among hybrids of *Populus balsamifera* and *P. angustifolia* because they both belong to section *Tacamahaca*. Since it is not possible to make discrete divisions based on species, overlapping groups corresponding to species composition can be constructed. In this way, error due to misplaced intermediary forms is reduced. Other continuous characters that require the same treatment include the phenology of flowering, leaf flush, leaf senescence, and leaf fall. After division by phenology, the remaining characters can be incorporated similarly. The most interesting, and probably the most useful of the last characters is the susceptibility to insect injury. It too is a continuous character so overlap in the categories is advised. Even with the increasing redundancy of repeated entries, each successive partition narrows the field of potential clones.

The next step in clone delineation is to introduce the spatial element. In the study rationale, the convention for confident clone identification requires potential ramets to be spatially associated. Working within these confines, the spatial proximity of each group can lead to a decision on the likelihood of their clonal relatedness. In the case of redundant appearances in more than one clone group, an individual can be committed to the group with which it shares the most characteristics and the closest proximity. The final product of these manipulations will be a specific number of hypothesized clone groups with each tree designated as belonging to one clone or occurring as a singular trunk. These groupings and their characteristics can then be used to characterize the non-randomness and potential for clonality in such populations.

3.0 METHODS:

3.1 Study Site:

The selected study site is located within the city limits of Lethbridge Alberta, in the Oldman River floodplain. It consists of an artificial island defined by a diversion canal, which was excavated in 1956 to service the weir which extends across the river just below the University of Lethbridge campus. The maximum dimensions of the island are approximately 200 X 200 meters. Every cottonwood with a trunk circumference at breast height of greater than 10 cm was included. In total, 391 cottonwoods were included and numbered with aluminum tags which were nailed to the trunks at eye level.

To facilitate the mapping of the population, a grid with gradiations of 20 X 20 meters was superimposed over the area. This calibration was chosen so that the number of trees within any given square would not exceed twenty. The grid was oriented at right angles to the river channel. Each grid intersection was positioned using a surveyor's transit, and marked with a white stake to enhance visibility. Within each grid-box the position of every tree was mapped and referenced according to its tag number.

3.2 Half-siblings:

Half-siblings from each species were grown from seed sources on site to furnish the comparison of leaf shape characters. During the third week of June, 1994 and during the same period in 1995, one ripe catkin and several mature leaves were collected from each of a total of 18 female trees; 9 each year. Estimations of the species-types of these trees were made based on the leaf samples. There were 5 *Populus angustifolia*, 3 *P. angustifolia* X *P. balsamifera*, 2 *P. balsamifera* X *P. angustifolia*, 1 *P. balsamifera*, 4 complex tri-specific hybrids, and 3 *P. deltoides*. A selection of seeds were extracted from each catkin, each seed was separated from its pappus, and immediately germinated together with its siblings on moistened filter paper in a petri dish. Within a few days, a random selection of viable seedlings from each group were transplanted to root-trainers containing sterile potting media in the University of Lethbridge Biological Sciences greenhouse and provided with identical environmental conditions. The seedlings grew rapidly, and after approximately one month, were transplanted to large pots. After at least five months of growth, photocopies were made of three mature leaves collected between the first and fifth nodes from each of 247 individuals. The petiole length, blade length, blade width, angle of blade edge from petiole, distance from base of blade to position of maximum blade width, and maximal tooth depth was measured for every leaf. After being standardized to a blade length of 10 cm., these dimensions were analyzed for individual and group variation.

3.3 Data Collection:

3.3.1 Physical observations:

The maps of every grid section were compiled to construct a complete site map. This representation was digitized to generate X and Y coordinates for each tree. Trunk circumference was measured at breast height on every tagged trunk. Miscellaneous observations were recorded regarding health and environmental effects. Connectivity of neighboring trunks was also recorded. Trunk architecture was designated 'straight' if there was a single, upright leader-branch, from which smaller branches originated, and the entire form displayed a strong vertical tendency, 'gnarled' if such a leader-branch was absent and the branches tended to spread as far horizontally as vertically, or 'twisted' when there was at least one, fairly vertical, main leader-branch but the other branches tended to spread horizontally as well as vertically.

3.3.2 Morphological characteristics:

For every tree which flowered in 1995, a determination of sex was made according to floral characteristics observed through binoculars. These sexes were re-checked in subsequent surveys of phenology.

Approximately six mature leaves (from first and second node positions) were collected and photocopied for every tree. Eight leaves were selected from the population to characterize the range of leaf-shape variation present (Fig. 3-1). These were coded from 1 to 8, with 1 representing pure *P. angustifolia*, 4 being pure *P. balsamifera*, and 8 as pure *P. deltoides*. Each set of leaves was classified according to the selected leaf shapes. An intermediate code was used if the shape was transitional; for example a leaf shape halfway between 2 and 3 was coded 2.5. It should be remembered that this coding

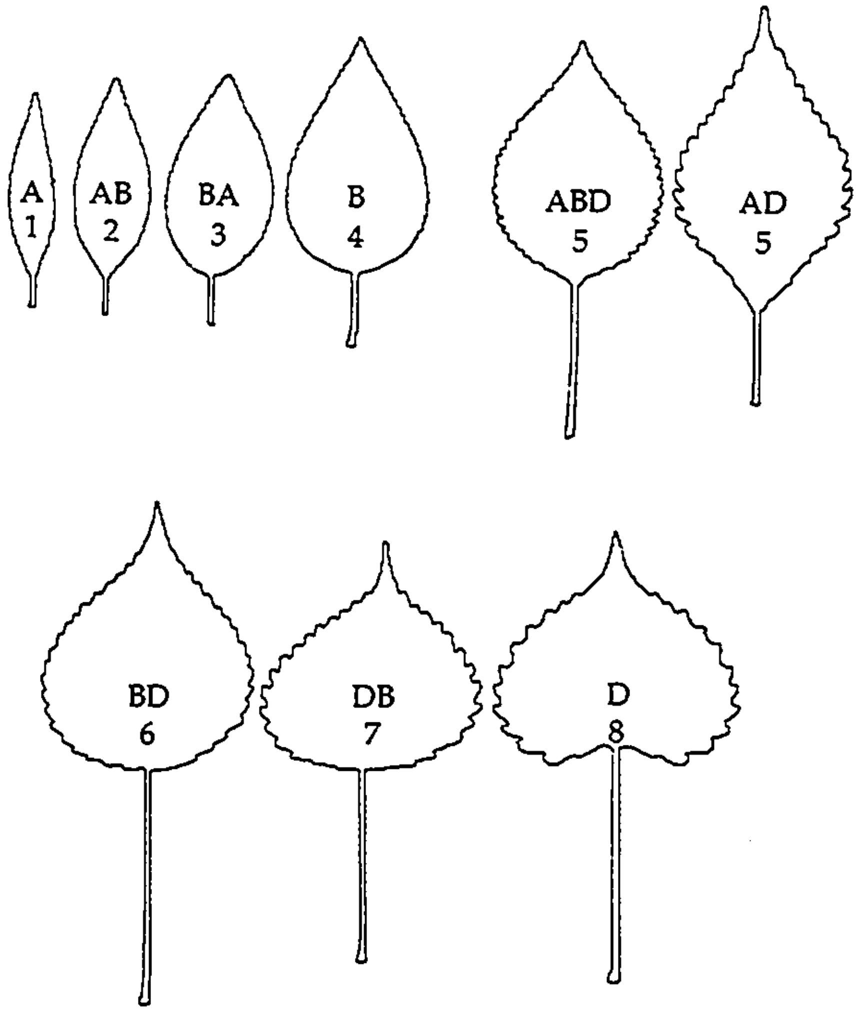
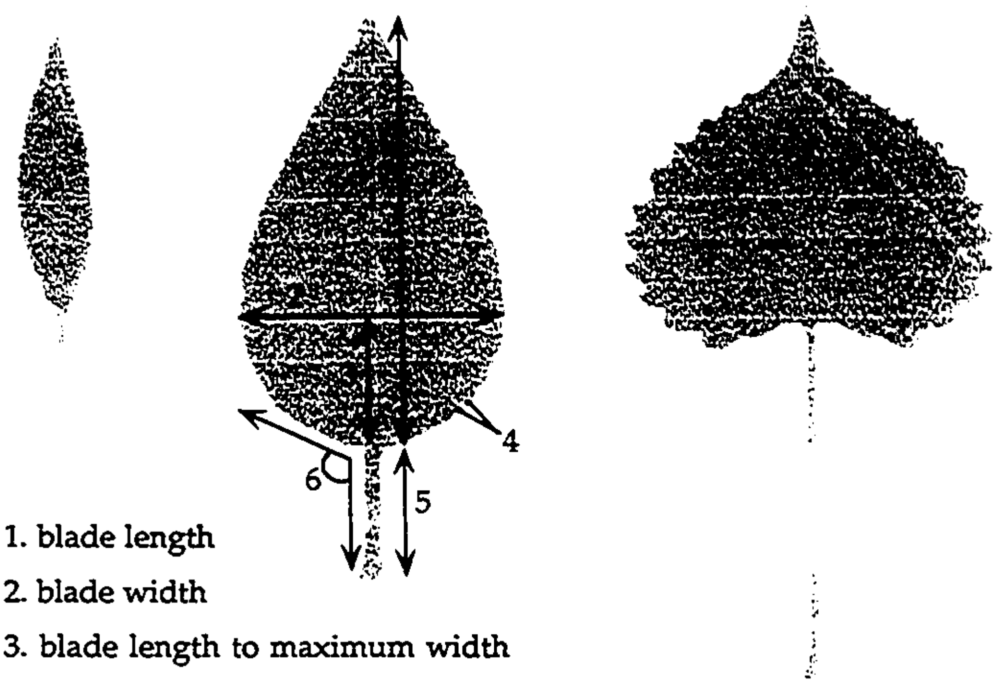


Figure 3-1. Typical leaf shapes selected from the study population to guide leaf-shape classification. Letter codes indicate hypothesized species composition; A = pure *Populus angustifolia*, B = pure *P. balsamifera*, D = pure *P. deltoides*, and mixed letter combinations indicate hybrid composition with the first letter indicating the predominant species, except for ABD and AD which represent complex hybrids lacking a predominant species. The numbered codes are introduced for simplicity in record keeping and analysis.

system was developed as a convention for this project, and detailed species identification was not intended. Three of the photocopied leaves were selected randomly from each tree's records and measured for blade length, petiole length, blade width, distance from base of blade to position of maximum blade width, maximum tooth depth, and the outside angle from petiole to the blade base (Fig. 3-2).



1. blade length
2. blade width
3. blade length to maximum width
4. tooth depth
5. petiole length
6. angle from edge of blade to petiole

Figure 3-2. Description of the six leaf measurements recorded from each of three mature leaves from each tree. For efficiency, the dimensions of photocopies of the leaves were digitized directly into a database.

In conjunction with Kalischuk et al. (submitted), a survey of *Aceria parapopuli* (Keifer) galls occurring within this population was conducted on February 9 and 16, 1996. Gall abundance per tree was estimated by the number of galls counted during a one minute interval through binoculars. The count reached its saturation point at approximately 130.

3.3.3 Phenological characteristics:

The phenological characteristics of interest here involve timing and duration of flowering, leaf flush, leaf senescence, and leaf drop. To capture the timing of these phenological events, surveys of the entire population were conducted in the spring of 1995 on May 2, 5, 8, 10, 13, 17, 19, 23, 25, and June 1, and in the autumn of 1995 on September 13, 20, 27, October 4, 11, and 19. Although phenological changes occur on a continuous scale, it was necessary to impose their division into discrete stages for the purposes of this investigation. The number of stages used to describe each type of phenology was decided by the number of phases that were distinguishable through binoculars.

Stages 0 through 4 of male and female flower-expansion and development are described in Fig. 2-1 and Fig. 2-2. Flowering stage 5 was used where the catkins had fallen from the tree. In males, flowering stage 5 is developmentally equivalent to stage 4, and in females, stage 5 would follow capsule ripening and seed release so was not observed before June 1. Bud break and leaf expansion were coded 0.5, 1, and 2, for initial bud break, leaf emergence, and leaf expansion respectively (Fig. 3-3). Leaf senescence was coded 0, 5, 10, 15, 20, 25, 50, 75, 99, or 100 % for each tree according to the estimated ratio of yellowed foliage. These percentages were coded 0 through 9 respectively for easier graphic analyses. Leaf drop was coded 0, 5, 10, 25, 50, 75,

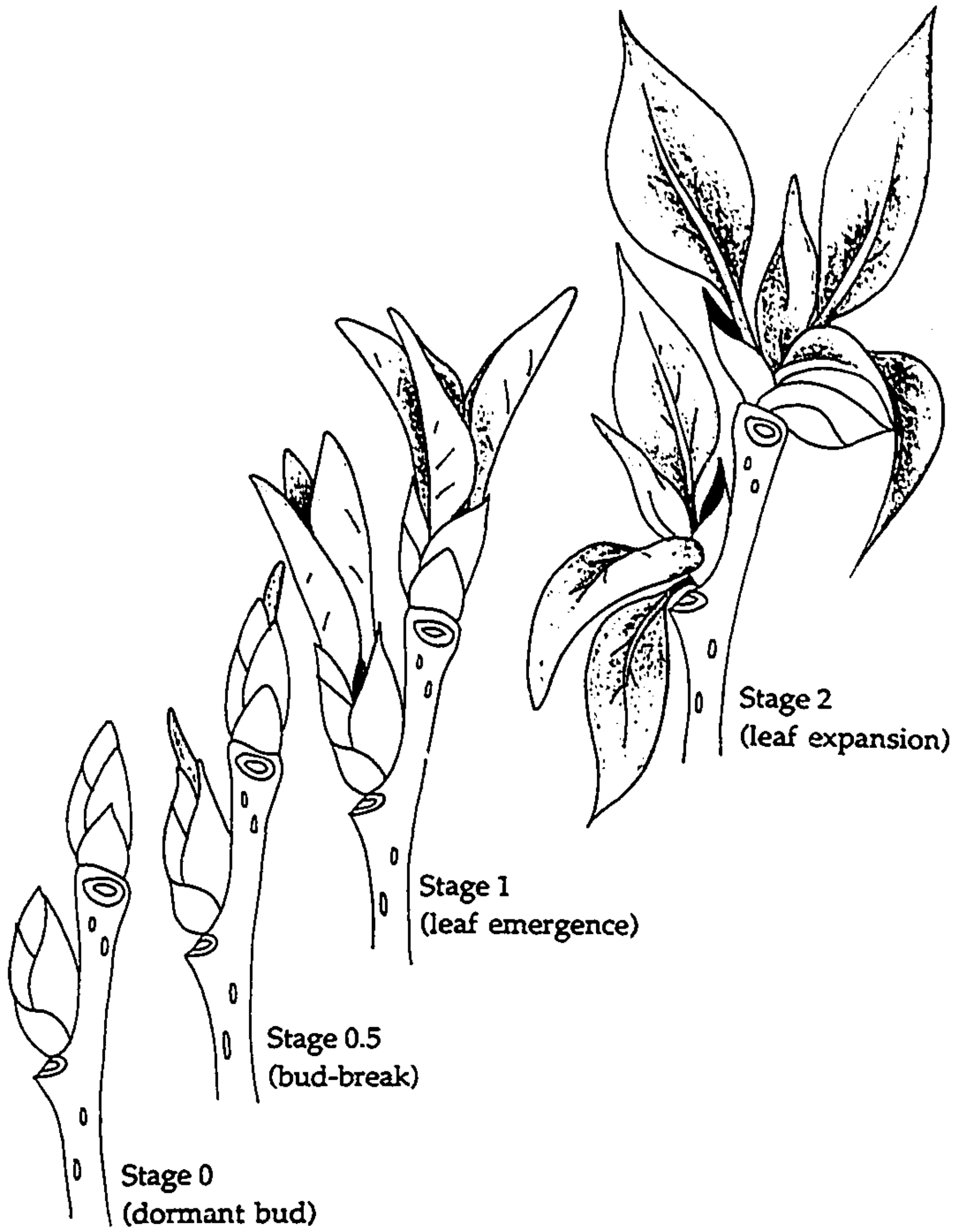


Figure 3-3. The four leaf-flushing stages in cottonwoods.

99, or 100 % for each tree according to its estimated ratio of leaves dropped. These percentages were coded 0 through 7 respectively for easier graphic analyses. Branch sacrifice (cladoptosis), where select branches senesce prematurely compared to the rest of the tree, is thought to be species dependent and directly influenced by water stress, but it was nonetheless recorded as 1, 2, or 3 depending on the number of branches affected.

3.4 Treatment of the Data:

To evaluate the likelihood that clonality is responsible for the nature and distribution of characteristics within this cottonwood population, the properties of the characteristics were statistically analyzed. Analyses included the Chi-square test for goodness of fit, Chi-square test of independence, F-Test, t-Test, and ANOVA. Calculations for the Chi-square tests were conducted according to Ambrose and Ambrose, 1977. The F-Test, t-Test, and ANOVA were calculated using the Microsoft Excel, version 5.0, Analysis Toolpak. Scatterplots and line-graphs were used extensively for descriptive purposes.

A method devised and described by Clark and Evans (1954), for characterizing spatial distributions as clustered, random, or uniform using nearest neighbor distances was also utilized. It uses a density value to predict the potential for nearest neighbor distances. By analyzing known density and nearest neighbor distances, the method matches the tested distribution with one of the three model spatial distributions to reach a decision. To apply this technique to the present study, a measure of site size was necessary for the density calculations. Every 20 X 20 meter grid-square surveyed was included in the first set of calculations to make a total area of 28 400 m^2. In the second set, grid-squares without trees were disregarded to prevent including areas unsuitable for cottonwoods, so the total area was 22 400 m^2.

The X - Y coordinate system, indexing the location of each tree, was translated from the arbitrary-units of the digitizing tablet into meters. The distances between every tree and every other tree were then calculated by applying the Pythagorean theorem to each combination of X - Y coordinates. In this way, the neighbors of every tree were cataloged in order of proximity with their distances for later analysis.

4.0 RESULTS AND DISCUSSION:

4.1 Characteristics of the Population:

4.1.1 General description:

Spatial distribution of trunks:

The spatial arrangement of the population is illustrated in Fig. 4-1. To investigate the randomness of this distribution, the distances from every tree to every other tree were calculated by applying the Pythagorean theorem to each combination of X, Y coordinates. The resultant matrix of distances identified every individual's neighbors in order of proximity. The two extreme outliers whose nearest neighbor distances exceeded 20 meters were removed, and the trends were calculated from the remainder. The average distances to the first, second, and third-nearest neighbors were found to be 1.98, 3.61, and 4.91 meters respectively. Considering the large size of the study site, these distances suggest a high degree of clumping.

Results and examples from the Clark and Evans (1954) method of analyzing spatial distributions can be viewed in Table 4-1. Special attention should be paid to the R statistic, which summarizes the distribution. For both the entire site and conservative area, the spatial distribution of trunks was obviously clustered (non-random).

Trunk circumferences:

Trunk circumference measured at breast height was found to range from 10 to 261 cm. The frequency distribution of the circumferences is portrayed as a histogram in Fig. 4-2. It is suspected that the peak under 30 cm originated as suckers. Five size categories were mapped to depict the spatial distribution of circumference (Fig. 4-3). It is not obvious from this map whether trunk sizes occur in a predictable pattern. Successive years of seedling recruitment can cause the population to be youngest nearest the river and oldest farthest away. If trunk circumference is taken as a general index of tree age, a pattern of increasing circumference with increasing distance from the river would be expected. However, this relationship is not found when distance from the main channel is plotted against trunk circumference (Fig. 4-4). An alternate pattern of seedling establishment can result after a widespread recruitment event produces an evenly aged forest over an extensive area. The aforementioned scatterplot does not fit this model either because there are small trunks interspersed among the larger ones. Since cottonwood seedlings are not competitive, it is unlikely that the small trunks could have originated as seedlings under an already mature canopy. When the circumferences of nearest neighbors are compared (Fig. 4-5), there is a loosely-correlated, positive relationship with a high degree of scatter. This suggests that neighboring trees tend to have similar trunk circumferences.

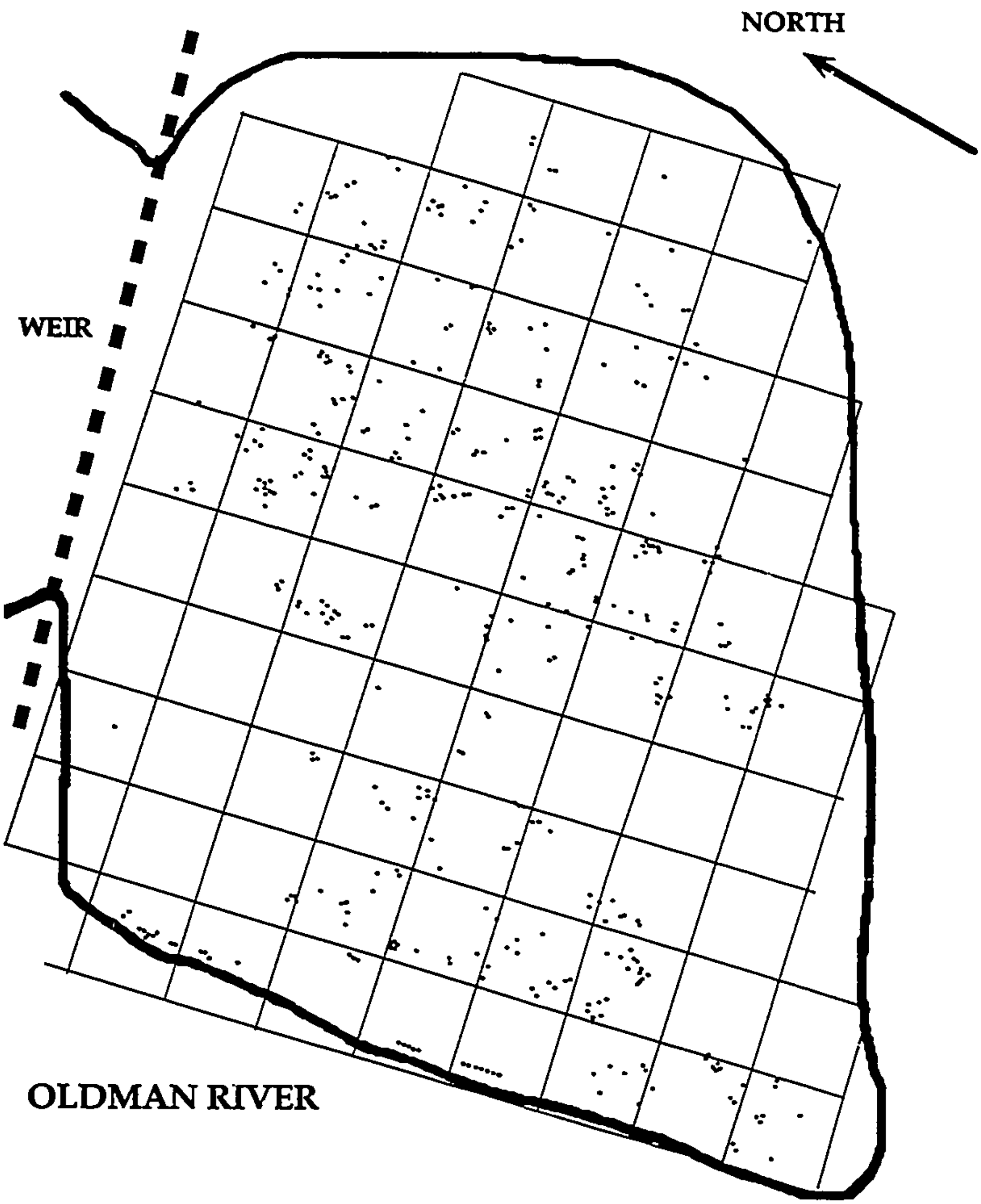


Figure 4-1. The spatial positioning of all cottonwoods measuring over 10 cm in trunk circumference at breast height in the research population (N=391).

Table 4-1. Deciding spatial pattern of distribution based on nearest neighbor distances; according to Clark and Evans 1954. Measurements for the synthetic random distribution were taken directly from Clark and Evans 1954, who made measurements from an artificial distribution of randomly arranged points. Values for the synthetic uniform distribution were generated by working back from the maximum R value of 2.1491, with density comparable to that on the research site. Note that R=0 under conditions of maximum aggregation, and R=1 where perfect randomness occurs. The entire site consisted of 71 subunits of 400 m^2 each. The conservative version of site area disregards 15 subunits (6 000 m^2) which are peripheral and have no trees.

Statistic	entire site	conservative area	synthetic random	synthetic uniform
Size of area . .	28 400	22 400	25 781	20 000
N	391	391	116	400
ρ	0.01376776	0.01745536	0.00449944	0.02
Σr	832.3501	832.3501	833.12	3039.2864
$\bar{r}_A$	2.12877268	2.12877268	7.1821	7.598216
$\bar{r}_E$	4.2612871	3.78447495	7.4540	3.5355339
R	0.49956096	0.56250146	0.9635	2.1491
$\sigma_{\bar{r}_E}$	0.11264749	0.10004292	0.3618	0.0924047
c	18.930864	16.549919	0.75	43.966185
p - value . . .	« 0.0004	« 0.0004	0.453254	« 0.0004
Decision:	clustered	clustered	random	uniform

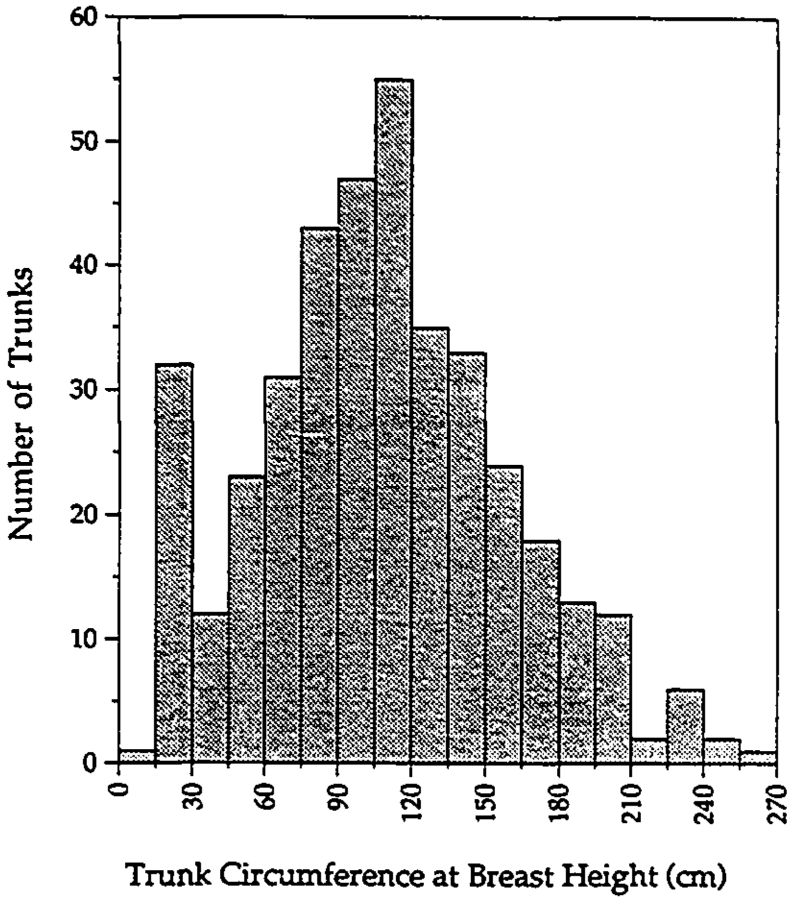


Figure 4-2. Histogram summary of trunk circumferences taken at breast height, for all trunks (N=391).

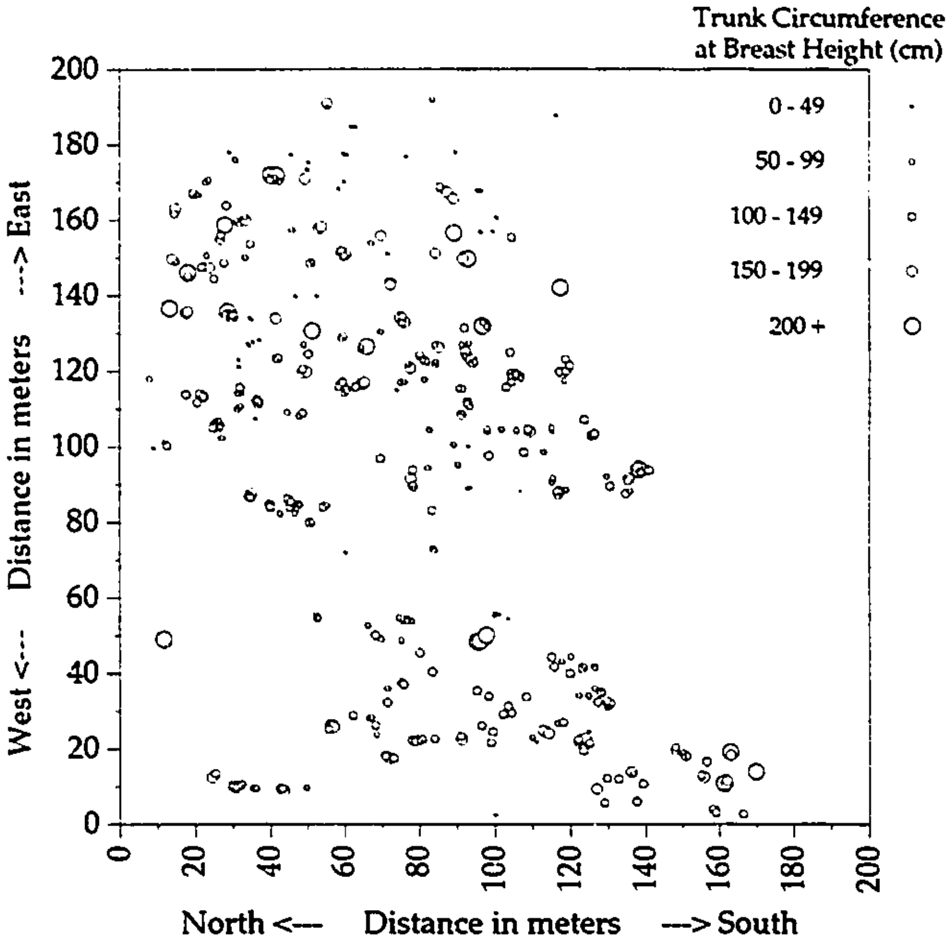


Figure 4-3. Spatial distribution of trunks classified according to five circumference categories (N=391).

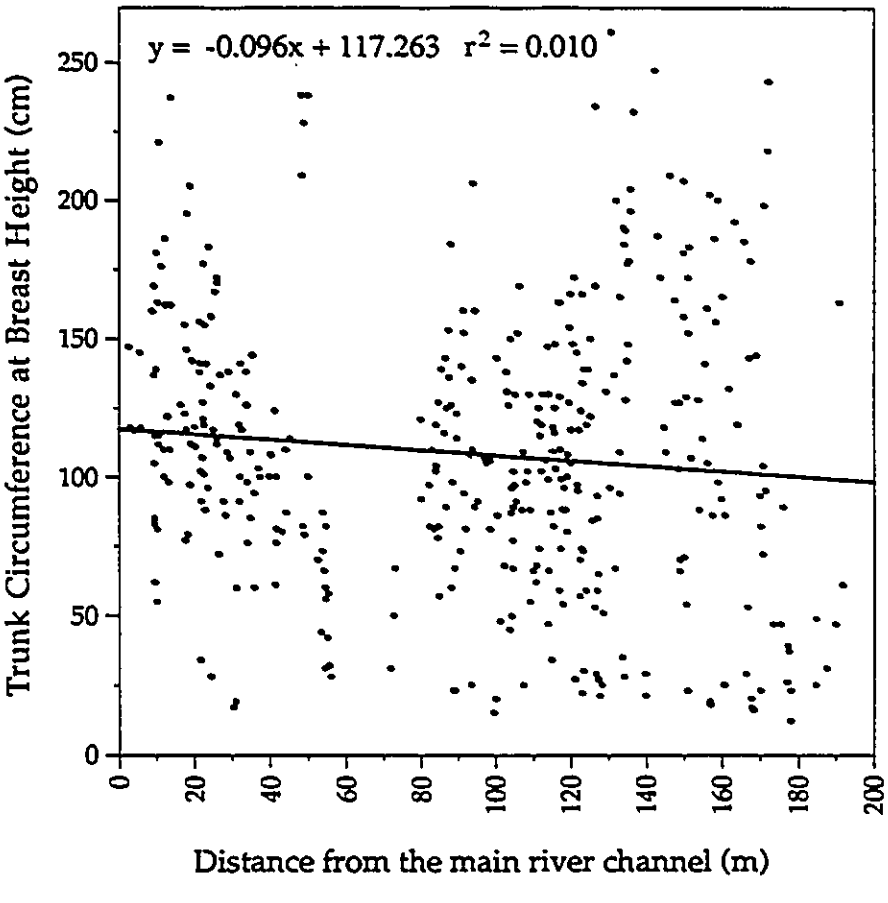


Figure 4-4. The relationship between distance to the main river channel and trunk circumference at breast height. The position relative to the river is not positively correlated with trunk circumference.

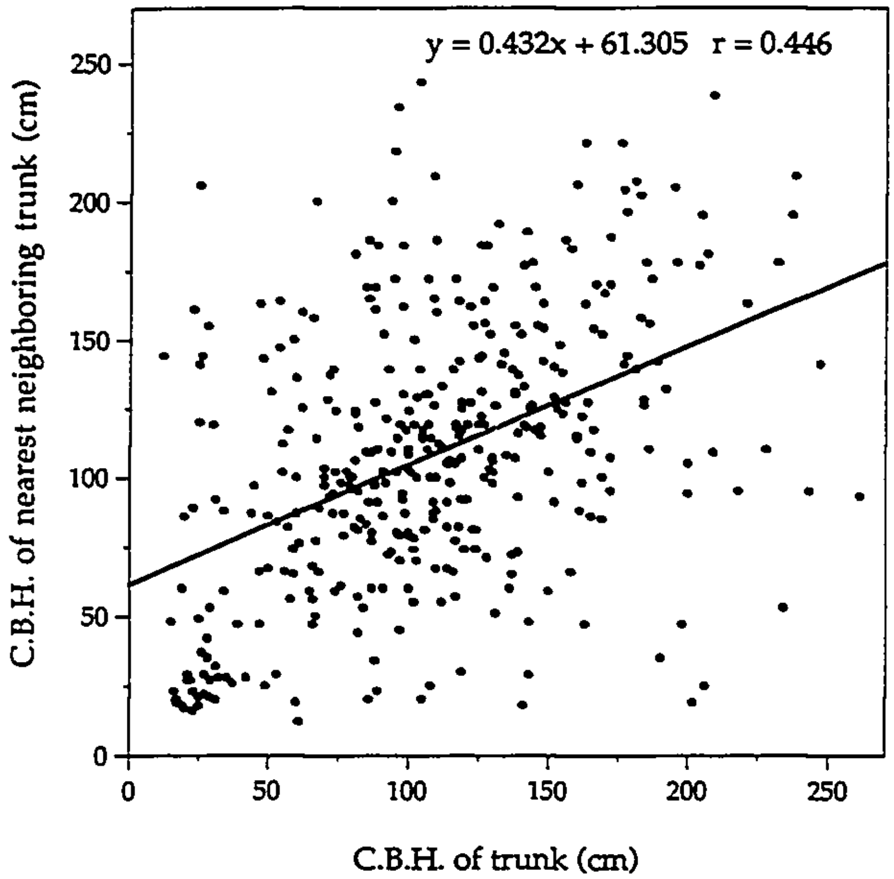


Figure 4-5. Comparing the trunk circumference at breast height (C.B.H.) of every tree with that of its nearest neighbor (N=391).

Beaver impacts:

During the period of study, beaver activity heavily impacted this stand of cottonwoods. Many main trunks were felled, and in most cases, sprouts were observed to initiate directly from their stumps. To summarize the spatial occurrence of beaver damage, degree of damage was categorized according to the proportion of trunk damage, and mapped spatially (Fig. 4-6). The majority of beaver damage occurred at the perimeter of the site since the river channel and diversion canal provide easy access for beaver. Using a chi-square test for independence, it was discovered that the nearest neighbors of beaver-affected trees have higher instances of beaver damage than those of beaver-unaffected trees (Table 4-2). Generally, beaver damage did not appear to be influenced by trunk circumference (Table 4-3). However, it did appear that severity of beaver damage was related to trunk circumference (Table 4-4), with smaller trunks being the most severely affected. Where sapling trunks are repeatedly felled, extensive stands of stump-sprouts proliferate, strongly influencing the pattern of clonal regrowth.

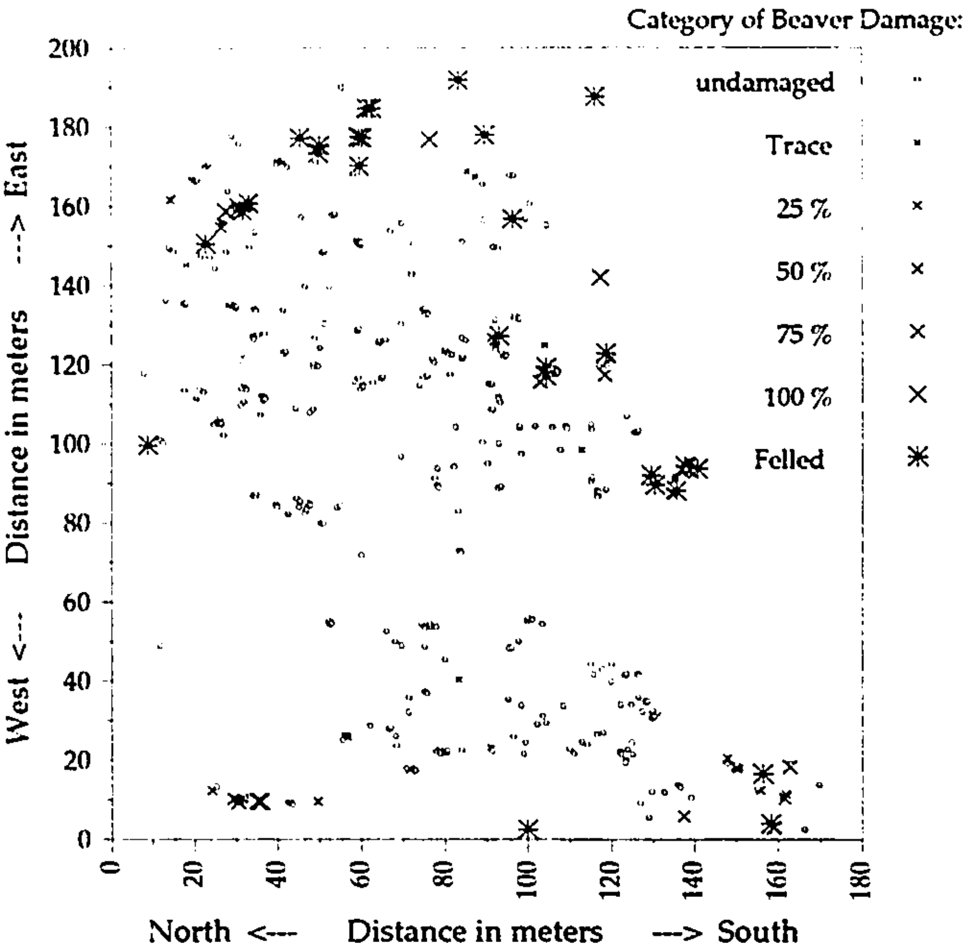


Figure 4-6. Spatial distribution of beaver damaged trunks. (N=391) Trace damage consists of minor tearing of the outer bark. The % values of damage estimate the degree of girdling (ie: 25 % indicates damage to 1/4 of the circumference). Note that the majority of beaver damage has occurred around the perimeter of the site since the river channel and diversion canal provide easy access for beaver.

Table 4-2. Using the X^2 Test of Independence: Do nearest neighbors of beaver-affected trees have higher instances of beaver damage than nearest neighbors of beaver-unaffected trees?

Contingency Table:		Nearest Neighbor Condition: affected:	unaffected:	Totals:
Beaver-unaffected:	Obs:	26	286	312
	Exp:	60.6	251.4	312
Beaver-affected:	Obs:	50	29	79
	Exp:	15.4	63.6	79
Column Totals:		76	315	391

Null Hypothesis: The nearest neighbors of beaver-affected trees have the same instance of beaver damage as those of beaver-unaffected trees.

$X^2 = \Sigma \{ [\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \}$ $\therefore$ $X^2 = 121.08$

df = 1 $\therefore$ critical X^2 value = 3.84 ($\alpha = 0.05$)

Since 121.08 » 3.84 $\therefore$ strongly reject the Null Hypothesis

(p-value >> 0.001)

Conclusion: The nearest neighbors of beaver-affected trees have higher instances of beaver damage compared to those of beaver-unaffected trees.

Table 4-3. Using the F-Test to determine whether the variance of C.B.H. in beaver-damaged trunks is significantly different from that in undamaged trunks, in order to choose the proper t-Test for testing whether the means of the two samples are significantly different (N=391).

F-Test: Two-Sample for Variances
Null Hypothesis: The two samples have the same variance.

	damaged	*undamaged*
Mean	108.96	107.89
Variance	2977.23	2527.96
Observations	78	313
Degrees of Freedom	77	312
F	1.1777	
P (F<=f) one-tail	0.1689	
F Critical one-tail	1.3258	

Decision: Do not reject the Null Hypothesis
Conclusion: The variances are not significantly different, therefore use the following t-Test:

t-Test: Two-Sample Assuming Equal Variances
Null Hypothesis: The two samples have the same mean.

Pooled Variance	2616.89
Hyp. Mean Difference	0
Degrees of freedom	389
t Stat	0.1658
P (T<=t) one-tail	0.4342
t Critical one-tail	1.6488
P (T<=t) two-tail	0.8684
t Critical two-tail	1.9661

Decision: Reject the Null Hypothesis
Conclusion: The means are not significantly different
-the C.B.H.'s of beaver damaged trunks are not significantly different from undamaged ones.

Table 4-4. Using an ANOVA to detect differences between the mean C.B.H. of three categories of beaver-damaged trunks; trace damage to 25% girdled, 50% to 75% girdled, and 100% girdled to completely felled.

SUMMARY:

Categories	*Count*	*Sum*	*Average*	*Variance*
T+25%	33	4343	131.61	1745.25
50+75%	10	1286	128.60	1034.49
100%+F	35	2870	82.00	3466.69

ANOVA: Single Factor

Null Hypothesis: The three categories have the same mean C.B.H.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between categories	46220.61	2	23110.30	9.4701	0.000215	3.1186
Within categories	183025.78	75	2440.34			
Total	229246.38	77				

Decision: Reject the Null Hypothesis

Conclusion: The mean C.B.H.'s of the three categories of beaver-damaged trunks are significantly different.

-The most severe category of beaver damage tended to contain trees of smaller mean C.B.H.

4.1.2 Directly clonally-conserved characters:

Characteristics vary in their degree of heritability. There are strictly, genetically-determined traits over which the environment has no influence, such as cottonwood sex and species, as well as characters which are less conserved because they are more environmentally sensitive. The stronger a character's conserved nature, or heritability, the better its reliability in clone delineation. The selected cottonwood characters in order of decreasing conservative nature are sex, species, and the timing of flowering, leaf flush, leaf senescence, and leaf drop. Discussions of their trends and patterns of spatial distribution follow.

Tree sex:

Tree sex is particularly useful in clone delineation because of its obligate heritability. The spatial distribution of the sexes is depicted in Fig. 4-7. The site contained a total of 204 females, 116 males, and 71 trees of unknown sex. When tested, the female to male sex ratio was not significantly different from 2 : 1 (Table 4-5 a and b). However, if the 71 unsexed trees were considered male, the sex ratio would not be significantly different from 1 : 1 (Table 4-5 c). The majority of these unsexed trees did not flower due to immaturity, so if the sex ratio was male-biased among immatures, then the 1 : 1 sex ratio might still be supported. However, of the trees under 50 cm in circumference that did flower, there were 9 females and 10 males, so it is unlikely that small, unsexed trees are exclusively male. Thus, the final ratio of females to males appears to approach 2 : 1 rather than 1 : 1. This type of ratio is consistent with findings for related species. Mosseler and Zsuffa (1989) observed female biased sex-ratios in their artificial hybridization studies of 8 Salix species, and female biased ratios have also been documented in populations of willow species (Crawford and Balfour 1983, Alliende and Harper 1989, Shafroth et al. 1994).

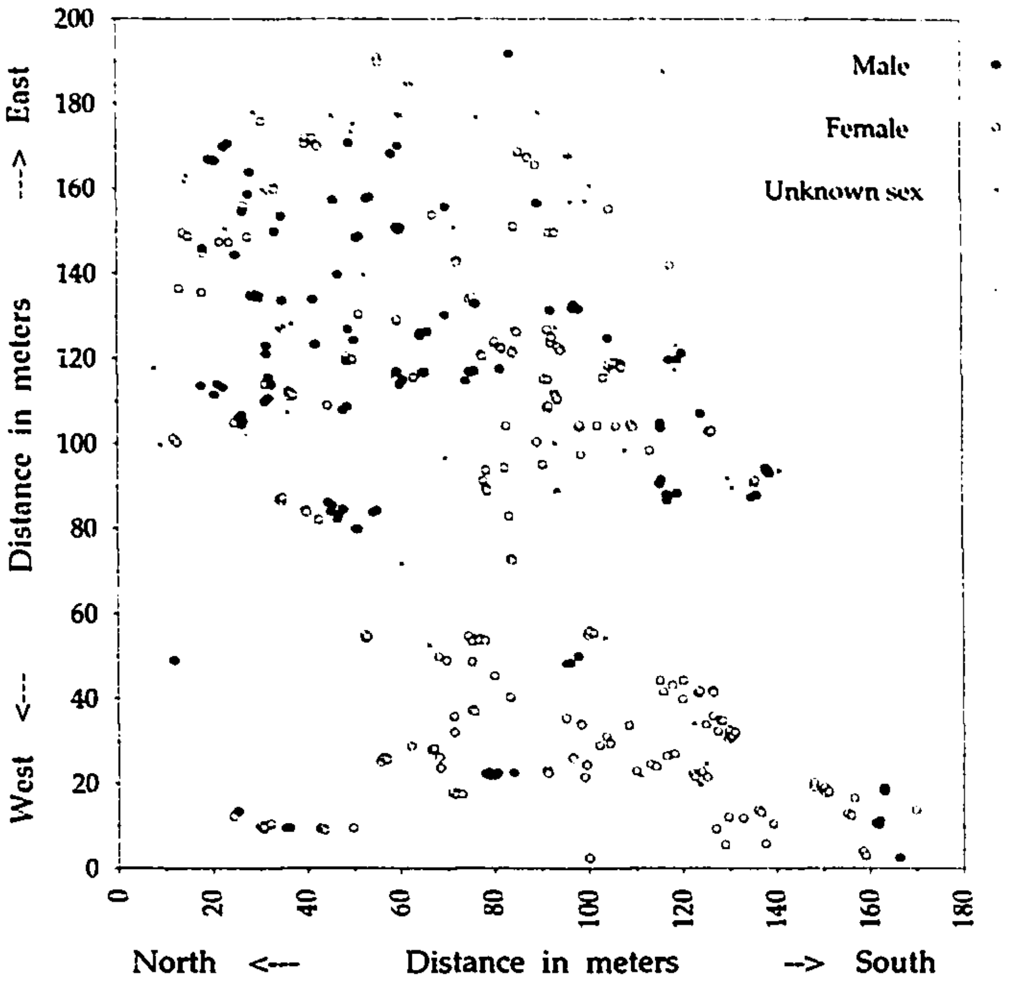


Figure 4-7. The spatial distribution of the 116 males, 204 females, and 71 trees of unknown sex.

Table 4-5. Using the X2 Test of Independence: Is the sex ratio equal or biased? (N=320, because 71 trees did not flower and so could not be sexed).

a) Null Hypothesis: The female to male ratio is 1 : 1.

	Female	*Male*	*Total*	*(unknown sex)*
Observed	204	116	320	(71)
Expected	160	160	320	

$X^2 = \Sigma\{[\text{Obs.} - \text{Exp.}]^2 / \text{Exp.}\}$ $\therefore X^2 = 24.20$

df = 1 $\therefore$ at $\alpha = 0.05$, the critical X^2 value = 3.84

Since $24.20 \gg 3.84$ $\therefore$ strongly reject Null (p-value=$\ll .001$)

Conclusion: female to male ratio is significantly different from 1 : 1.

b) Null Hypothesis: The female to male ratio is 2 : 1.

	Female	*Male*	*Total*	*(unknown sex)*
Observed	204	116	320	(71)
Expected	213.3	106.7	320	

$X^2 = \Sigma\{[\text{Obs.} - \text{Exp.}]^2 / \text{Exp.}\}$ $\therefore X^2 = 1.22$

df = 1 $\therefore$ at $\alpha = 0.05$, the critical X^2 value = 3.84

Since $1.22 < 3.84$ $\therefore$ fail to reject the Null Hypothesis (p-value = 0.3641)

Conclusion: female to male ratio is not significantly different from 2 : 1.

c) Null Hypothesis: The female to male ratio is 1 : 1
(when trees of unknown sex are assumed to be male)

	Female:	*Male + ? Sex:*	*Totals:*
Observed:	204	187	391
Expected:	195.5	195.5	391

$X^2 = \Sigma\{[\text{Obs.} - \text{Exp.}]^2 / \text{Exp.}\}$ $\therefore X^2 = 0.7391$

df = 1 $\therefore$ at $\alpha = 0.05$, the critical X^2 value = 3.84

Since $0.7391 < 3.84$ $\therefore$ fail to reject the Null (p-value = 0.3495)

Conclusion: female to male ratio is not significantly different from 1 : 1 (if trees of unknown sex are assumed to be male).

Other characteristics may be related to sex. An analysis of variance found that the sexes did not differ significantly in trunk circumference (Table 4-6). In Fig. 4-7 the spatial distributions of the sexes do appear to differ. It appears that females occur closer to the river channel than males. The test of this hypothesis is shown in Table 4-7, and the results concur that females do tend to appear nearer to the river. Comtois et al. (1986) found a 1:1 sex-ratio in *P. balsamifera* in northern Quebec, but also found that female stands predominate in regions with maritime climates (5:1) and humid habitats (7:1). Skewed sex-ratios in trembling aspen populations have also been linked to elevational variation by Il'in (1973), and Grant and Mitton (1979) who both observed that females predominated at lower elevations, and males at higher ones.

Leaf-shape (species-category):

Leaf shape was used to classify the species composition of every individual within the study population. A total of eight shape groups were classified (Fig. 3-1). Each corresponds with a particular species or hybrid combination. The two leaf shapes designated as number five represent a group of complex hybrids with the same general form, but difficult to determine species contribution. The non-random, clustered spatial distribution of leaf shapes within the population is obvious. To present the trends simply, the leaf shape categories have been mapped in three figures; one for members of section *Tacamahaca* (Fig. 4-8), one for members of section *Aigeiros* (Fig. 4-9), and one for intersectional hybrids (Fig. 4-10). The leaf shapes of nearest neighbors suggested a strong degree of spatial clustering (Fig. 4-11). When tested, a significantly non-random pattern emerges in nearest neighbor leaf shape composition (Table 4-8).

Table 4-6. Using an ANOVA to detect differences between the mean C.B.H. of male versus female trunks.

SUMMARY:

Categories	*Count*	*Sum*	*Average*	*Variance*
Male	116	13720	118.28	2736.64
Female	204	24075	118.01	1969.16

ANOVA: Single Factor

Null Hypothesis: Male and female trunks have the same mean C.B.H.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between categories	5.04358	1	5.04	.00224	.96224	3.8709
Within categories	714452	318	2246.70			
Total	714457	319				

Decision: Fail to reject the Null Hypothesis

Conclusion: Males and females do not differ significantly in mean C.B.H.

Table 4-7. Using the F-Test to determine whether the variances of male versus female distances to the main river channel are significantly different, in order to choose the proper t-Test for testing whether the means of the two samples are significantly different.

F-Test: Two-Sample for Variances
Null Hypothesis: The two samples have the same variance.

	Female	*Male*
Mean	75.4743	106.0132
Variance	2705.7684	2007.1333
Observations	204	116
Degrees of Freedom	203	115
F	1.34808	
P (F<=f) one-tail	0.03887	
F Critical one-tail	1.32098	

Decision: Reject the Null Hypothesis
Conclusion: <u>The variances are significantly different,</u>
therefore use the following t-Test:

t-Test: Two-Sample Assuming Unequal Variances
Null Hypothesis: The two samples have the same mean.
(the mean distances of females vs. males from the main river channel are not significantly different)

Degrees of freedom	269
t Stat	5.5237
P (T<=t) one-tail	3.9136E-08
t Critical one-tail	1.6505
P (T<=t) two-tail	7.8271E-08
t Critical two-tail	1.9688

Decision: Reject the Null Hypothesis
Conclusion: <u>The means are significantly different</u>
<u>(females tend to occur closer to the river than males do)</u>

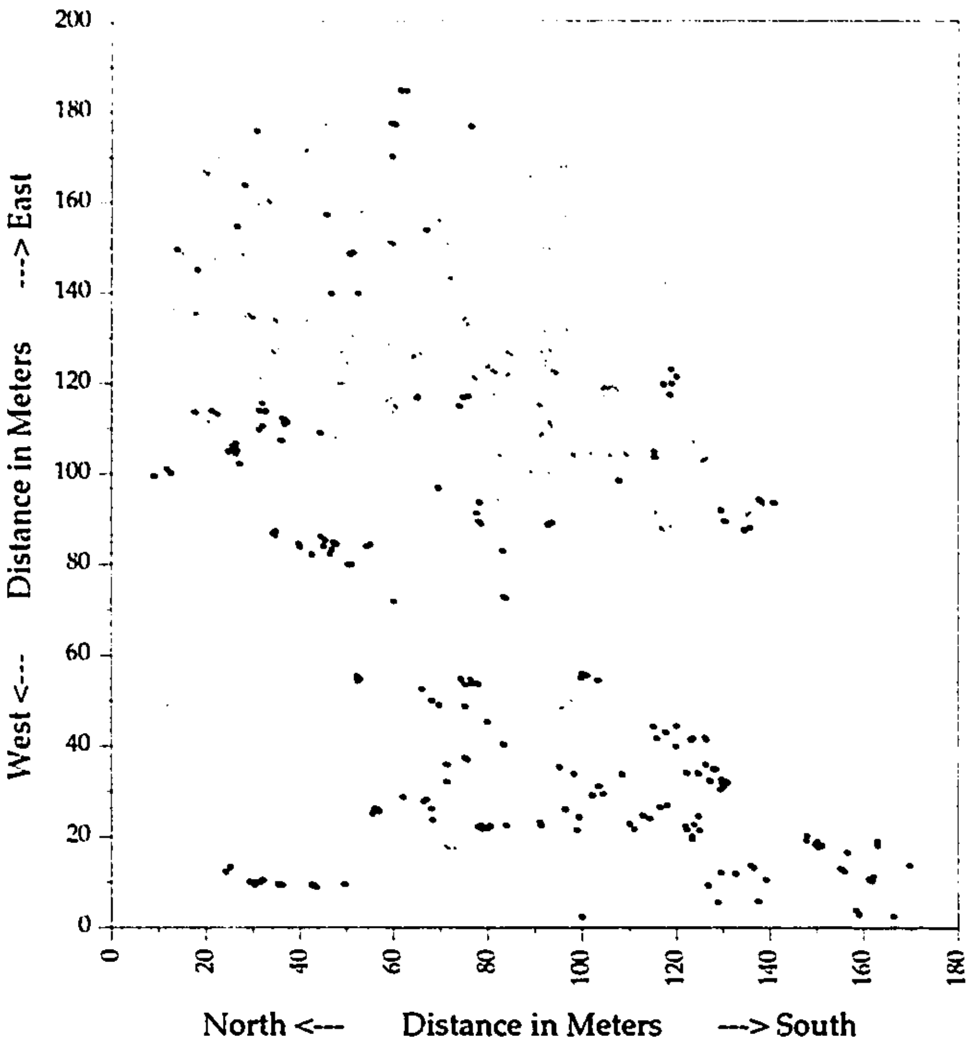


Figure 4-8. The spatial distribution of trunks with leaf shapes 1 to 4 (belonging to section Tacamahaca) shown as black circles, and leaf shapes 5 through 8 shown as grey X's (N=391).

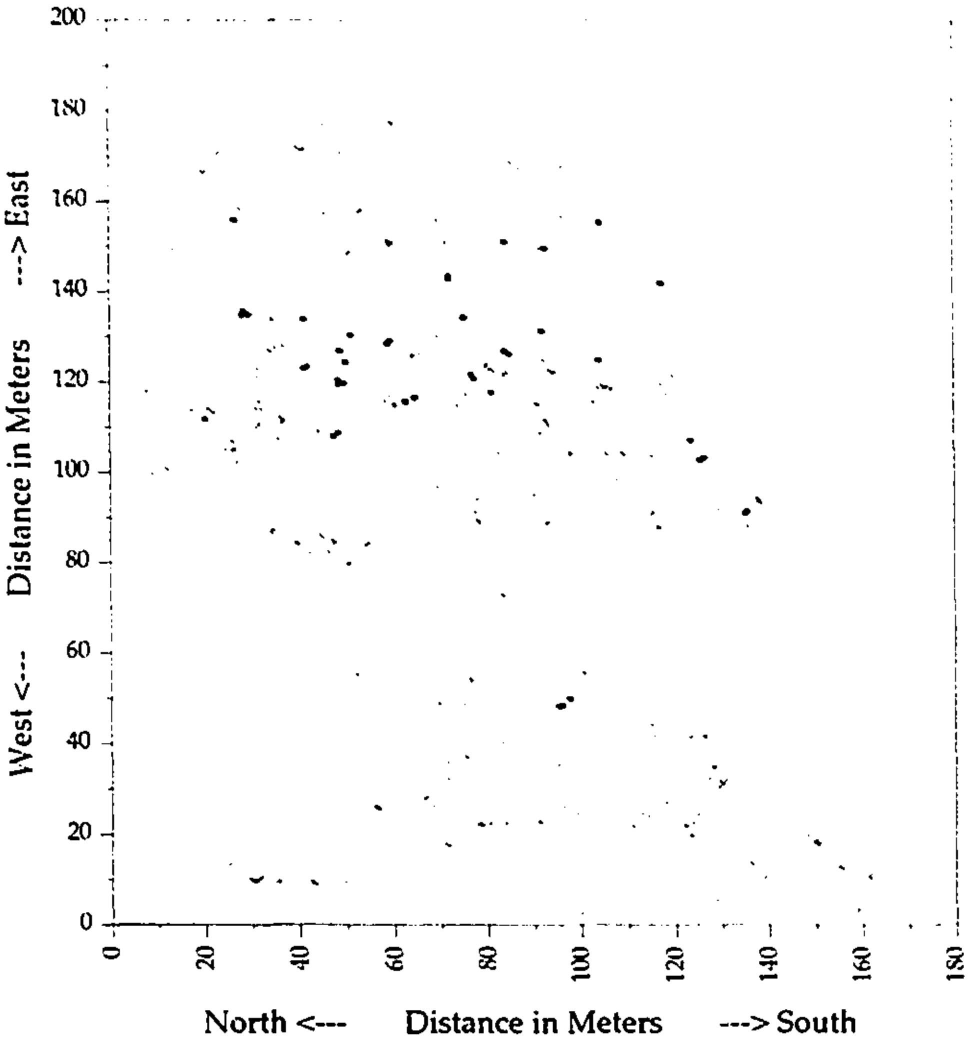


Figure 4-9. The spatial distribution of trunks with leaf shape 8 (belonging to section Aigeiros) shown as black circles, and leaf shapes 1 to 7 shown as grey X's (N=391) .

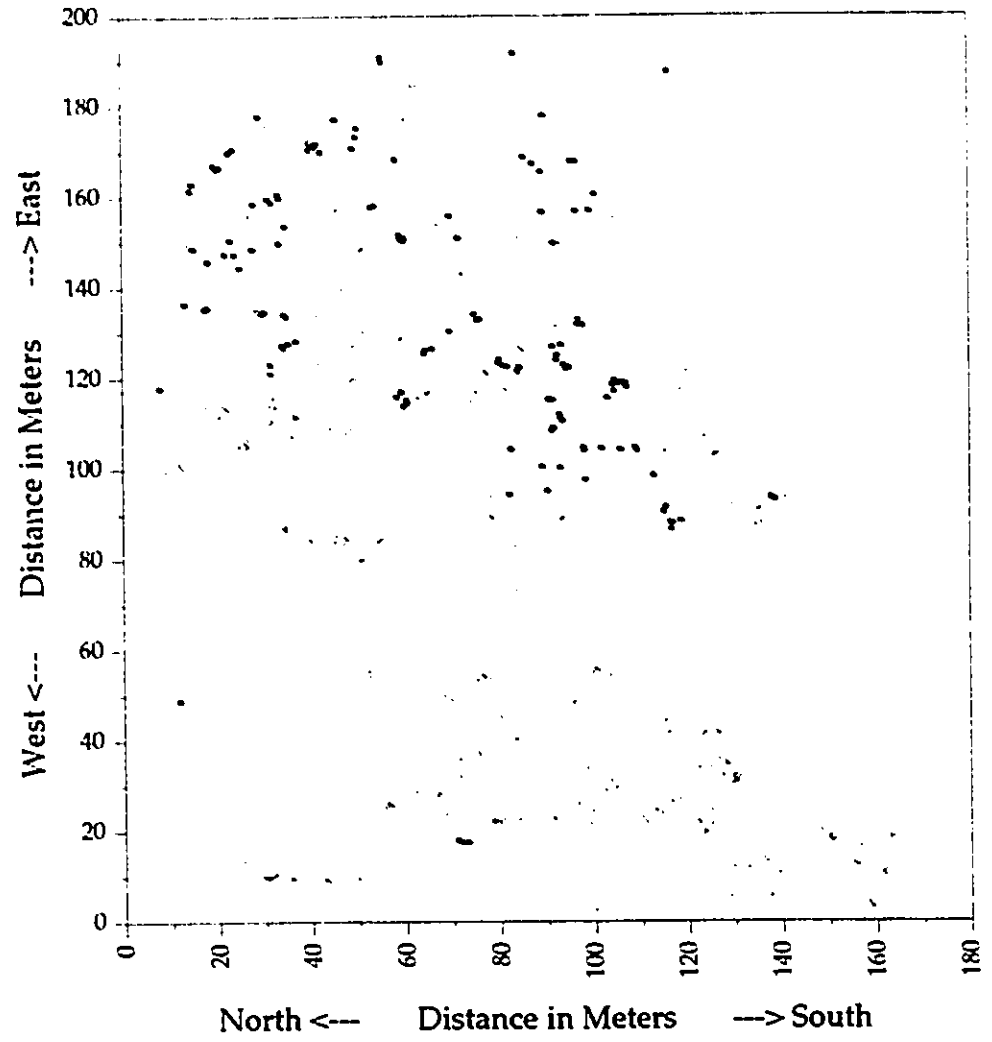


Figure 4-10. The spatial distribution of trunks with leaf shapes 5 to 7 (intersectional hybrids) shown as black circles, and leaf shapes 1 to 4 and 8 shown as grey X's (N=391).

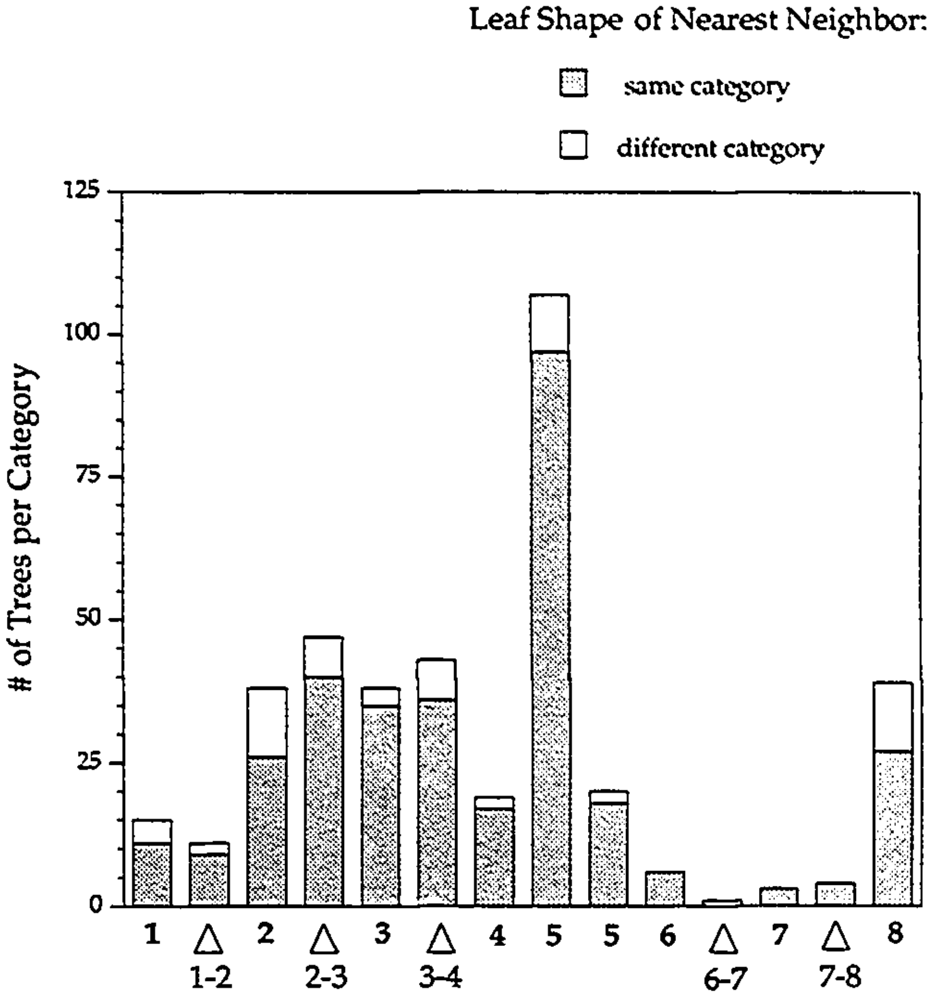


Figure 4-11. Summary of the study population's species composition as indicated by leaf shape (N=391). Hyphenated leaf shape codes indicate intermediate designations. Shading indicates instances where the leaf shape category of that tree's nearest neighbor was the same, or in an adjacent hybrid category.

Table 4-8. Using the X^2 Test for Goodness of fit: Do nearest neighbors have matching leaf shapes more often than randomly? Note that one degree of freedom yields a crit.$X^2 = 3.84$, and an * warns the expected value is < 5. Nearest neighbors with adjacent shape-codes were considered the same shape.

Null Hypothesis:

The occurrence of same-shaped nearest neighbor associations does not depart significantly from that expected due to random chance.

Leaf Shape Codes:		# of trees whose nearest neighbor is of the same leaf shape group:		# of trees whose nearest neighbor is of a different leaf shape group:			Significance of difference between the expected and observed:
		Expected	Observed	Expected	Observed	X^2	
1	A	* 1.00	11	14.00	4	107.45	* S
	A-AB	* 1.80	9	9.20	2	34.42	* S
2	AB	9.33	26	28.67	12	39.48	S
	AB-BA	14.79	40	32.21	7	62.74	S
3	BA	12.44	35	25.56	3	60.83	S
	BA-B	11.00	36	32.00	7	76.38	S
4	B	* 3.01	17	15.99	2	77.17	* S
5	ABD	34.75	97	72.25	10	165.11	S
	AD-BD	6.80	18	13.20	2	27.93	S
6	BD	* 0.41	6	5.59	0	80.89	* S
	BD-DB	* 0.03	0	* 0.97	1	0.03	* NS
7	DB	* 0.06	3	* 2.94	0	143.63	* S
	DB-D	* 0.47	4	* 3.53	0	30.00	* S
8	D	* 4.29	27	34.71	12	135.12	* S

Decision: Reject the Null Hypothesis

Conclusion: Frequently, the occurrence of same leaf shape nearest neighbor associations does depart significantly from that expected due to random chance.

Leaf dimensions:

Closely related to indices of leaf shape are measurements of leaf dimensions. The leaf dimensions measured in this investigation are described in Fig. 3-2. While general leaf shape is conserved, the size of leaves can vary dramatically within one individual. This potential for change in scale impairs the utility of direct comparison of leaf dimension measurements between leaves. By standardizing all leaf measurements proportional to one key measurement which is held constant for all leaves under consideration. Blade length is an appropriate constant since it represents a basic variable to which the other leaf dimensions are linked. Since the maximum blade length in the population approached 10 cm, this value was chosen as the constant. The standardizing procedure is illustrated in Fig. 4-12.

To minimize the chance of error due to unique variation in a single leaf specimen, three leaves were measured from every tree. To reduce these triplicate measures to a single set, a method for averaging each of the six measurements was sought. To prevent masking the important variation, averaging had to be conducted when the least variation occurred among the three leaves of an individual. To decide whether to average before or after the standardizing procedure, an average and standard deviation was calculated for the three leaves of each tree before and after standardizing for each of the six measurements. These values were then averaged to estimate overall variation. In Table 4-9, the columns labeled "Complete Average" contain the averaged averages, and those called "Complete St. Dev." contain the averaged standard deviations. For purposes of comparison, a relative measure of deviation was required, so the averaged standard deviations were translated into percent values relative to the averaged average in each case. The

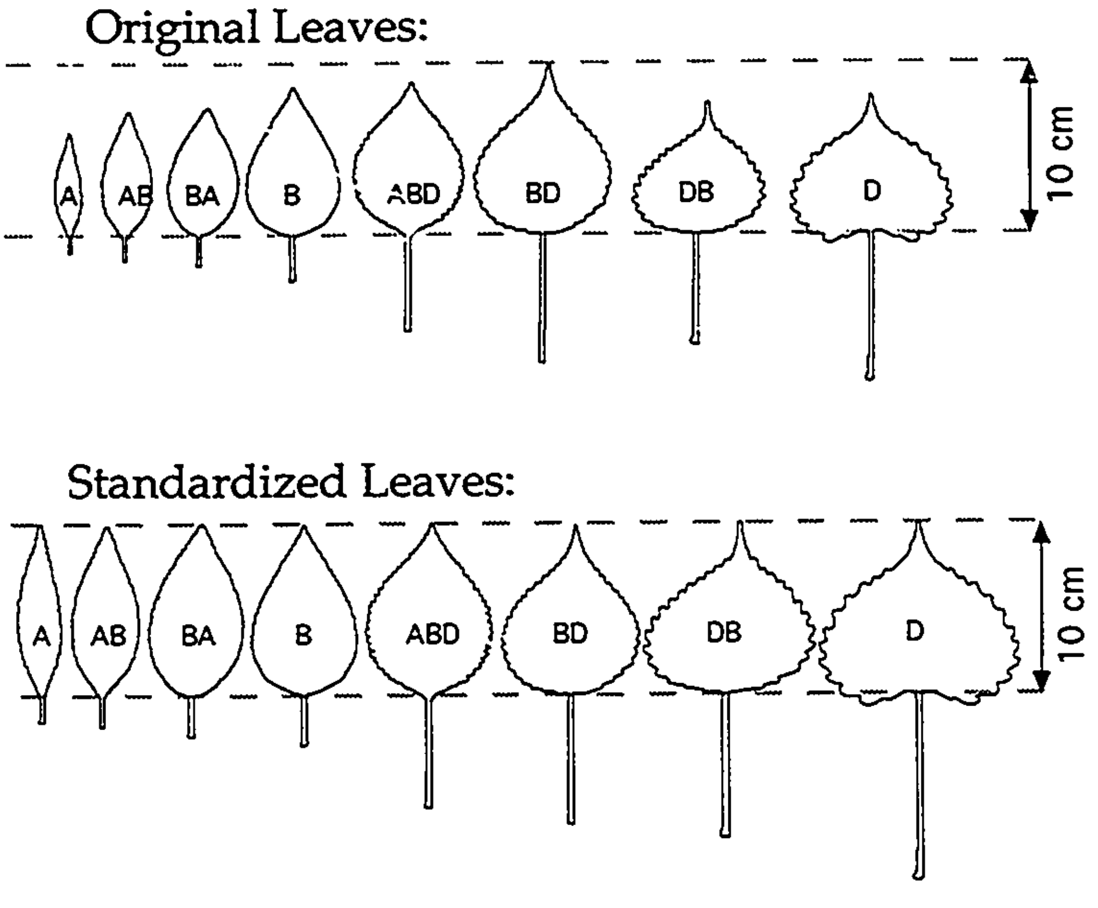


Figure 4-12. Illustrating the standardizing procedure. The dimensions of each leaf were adjusted proportional to a blade length of 10 cm. The eight leaf shape categories are depicted and labelled with their approximated species compositions.

Table 4-9. Computing the variation among the 3 leaves sampled for each tree before and after standardizing to determine whether it is more useful to average the measurements of the three leaves before or after standardizing them to a blade length of 10 cm (N=391). For each type of measurement, the average and standard deviation was found for the three leaves of each tree. These values were then averaged to estimate overall variation (see values labeled "Complete Average" and "Complete St. Dev."). For relative measures of deviation, the "Complete St. Dev." values were translated into percents relative to "Complete Average", these are labeled "Relative St. Dev". The same process was repeated following standardization.

	Actual Leaf Measurements:			Standardized Leaf Measurements:			Smallest
	Complete Average	Complete St. Dev.	Relative St. Dev. (%)	Complete Average	Complete St. Dev.	Relative St. Dev. (%)	Relative St. Dev.
Blade L:	6.28	0.56	8.93	10	0	0	Standard
Leaf L:	8.90	0.86	9.63	14.16	0.37	2.62	Standard
Petiole L:	2.62	0.35	13.33	4.16	0.37	8.93	Standard
Blade W:	3.95	0.35	8.85	6.30	0.39	6.22	Standard
Blade L.M.W.:	1.96	0.21	10.60	3.12	0.22	7.14	Standard
Tooth Depth:	0.11	0.01	10.91	0.17	0.12	71.50	Actual
Bl/Pet Angle:	117.65	5.57	4.73	(standardizing not required)			

Summary:

Since there is on average, less deviation between the measurements after standardizing, it would be more useful to standardize the measurements of the three leaves to a blade length of 10 cm before averaging them. An exception exists for the character of tooth depth, where it would be more useful to standardize after averaging the three leaf measurements together.

resultant values appear in the columns labelled "Relative St. Dev. (%)". The category with the smallest "Relative St. Dev. (%)" value produces the least variation among the leaves and so indicates the approach after which the three sets of leaf measurements should be averaged. In most cases there was less deviation after standardizing, so it was decided that the measurements should be standardized before averaging. An exception exists for tooth depth, where it would be more useful to standardize after averaging. These results emphasize that variation among the three leaves of a tree is due more to proportional size variation rather than to differences in leaf shape. For example, a particular tree may have large leaves with long petioles and small leaves with short petioles, however both types of leaves have the same shape despite a difference in size.

Once one set of six leaf measurements was decided for every tree, the population's trends in leaf dimensions could be analyzed. Fig. 4-13 summarizes the frequency distributions in each category of measurement. The patterns of peaks in each distribution can be traced to species-related distinctions and frequencies within the population. In particular, the distribution of standard petiole length shows three distinct rises, suggesting the population is comprised of groups with distinct forms. It should be noted that this type of standardized version of petiole length is equivalent to the ratio of blade length to petiole length and so is more informationally rich than either characteristic considered in isolation. Fig. 4-14 allows the inspection of relationships between the leaf measurements and leaf shape designations assigned earlier. The continuous variation in leaf measurements among *Tacamahaca* hybrids is obvious in these illustrations as seen in the first seven lanes of each graph. Noteworthy are the areas in standard tooth depth, petiole length, and blade width, where little or no overlap occurs between adjacent leaf shape categories. These gaps emphasize

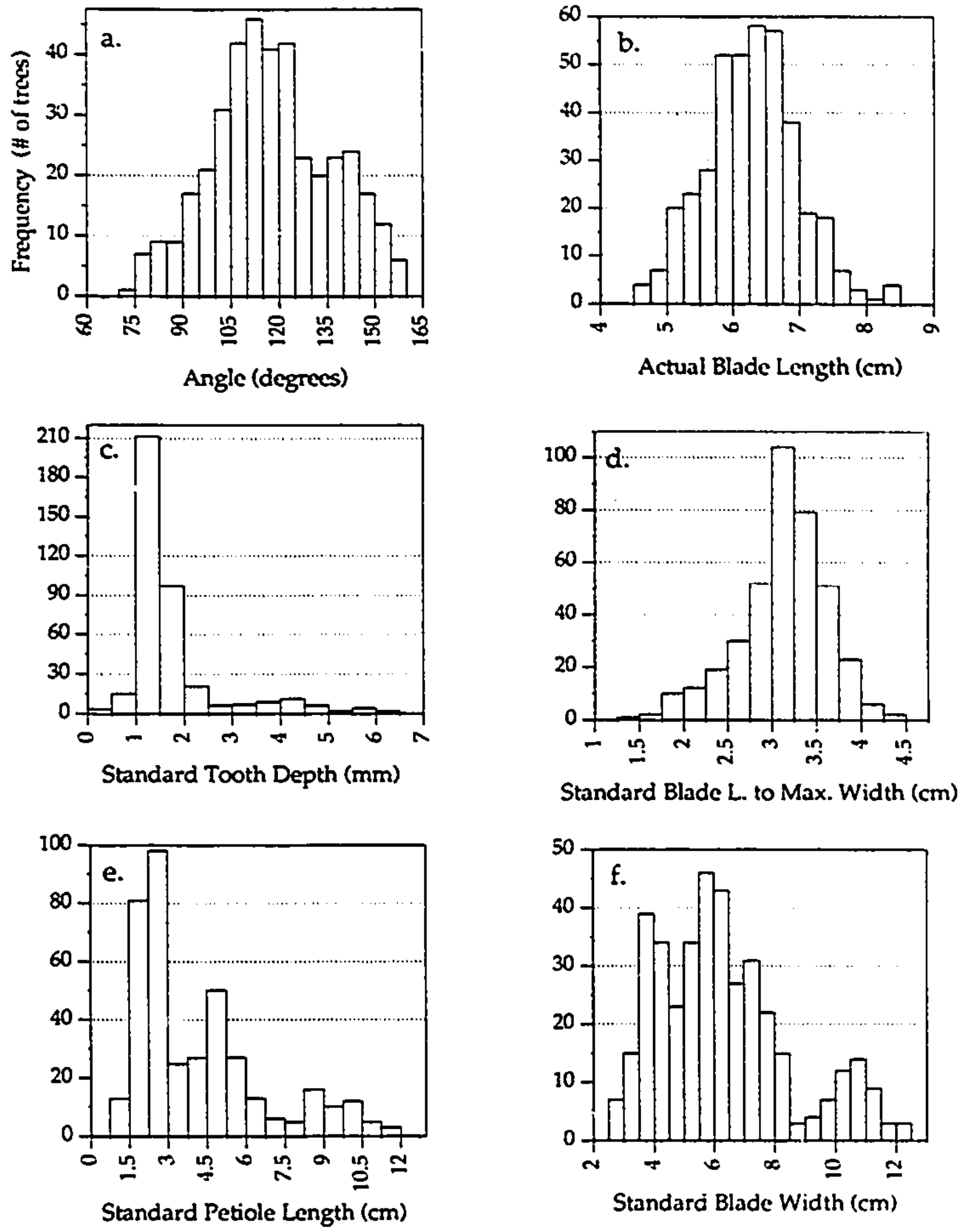


Figure 4-13. Summary histograms of actual and standardized (to a leaf blade length of 10 cm) leaf measurements averaged from three mature leaves per tree for every tree (N=391). The histograms depict; the angles from edge of blade to petiole (a), leaf blade lengths (b), and standardized values of tooth depth (c), distance from base of blade to position of maximum blade width (d), petiole length (e), and blade width (f).

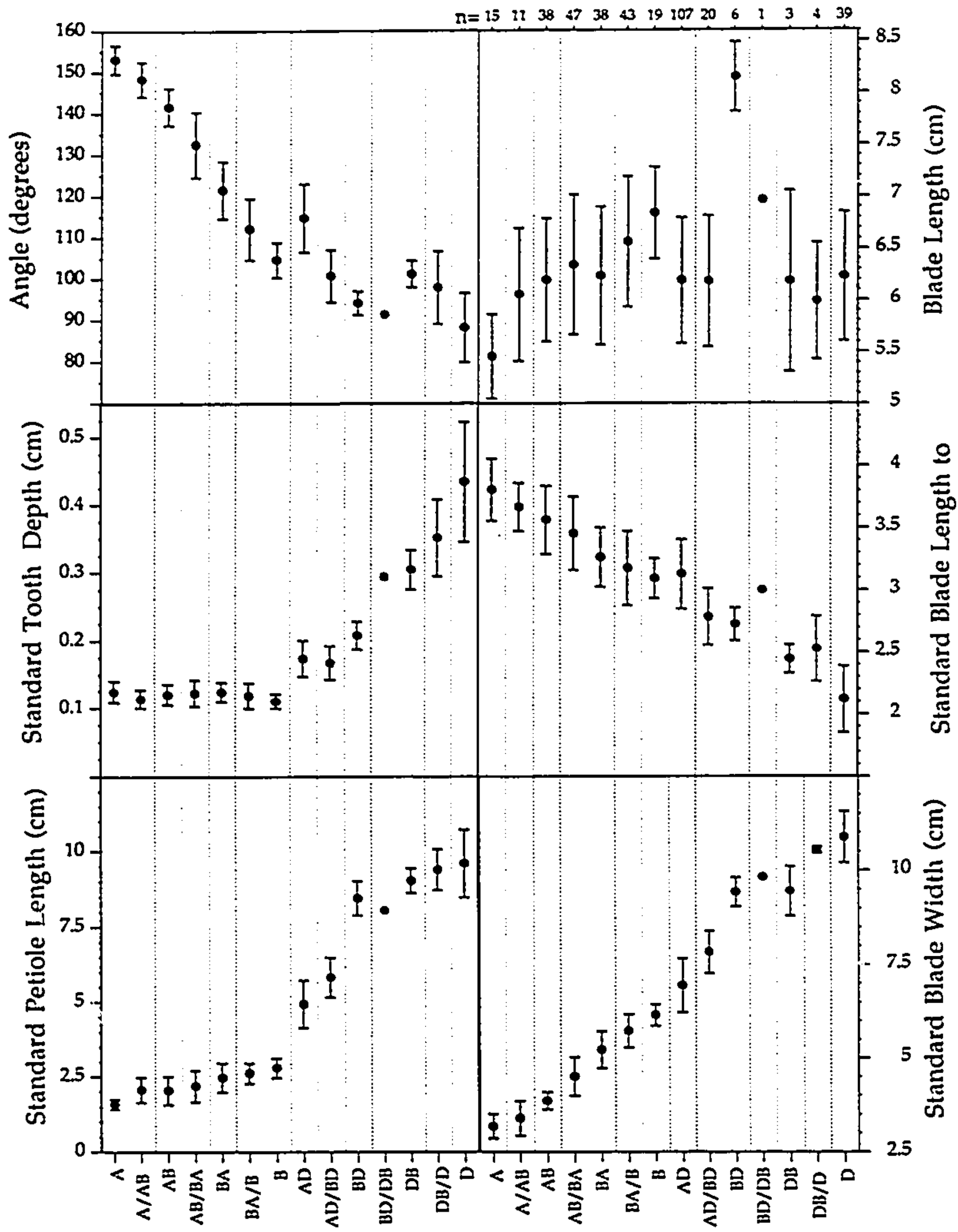


Figure 4-14. Trends in leaf measurements within the assigned leaf-shape categories. Error bars indicate one standard deviation. (N=391)

the existence of definable differences between the leaf-shape types. By considering select characters in concert, a more complete yet complicated picture emerges (Fig. 4-15). Vague clustering can be detected, but the scattering indicates a continuum of variation. The three main clusters can be generalized as section *Tacamahaca*, section *Aigeiros*, and intersectional hybrids. To summarize, these leaf measurements essentially serve to support the original leaf-shape based groupings.

In addition to sex and species, conserved characteristics of phenology can also be useful when investigating cottonwood clones. The patterns in timing of flowering, leaf flushing, leaf senescence, and leaf drop will be considered in this section. To optimize its utility in clone delineation, phenological variation in the population should range enough to allow individuality yet be limited within clones. To evaluate the application of phenology to clone delineation, the trends in the variability of these characteristics will be surveyed, and the potential for environmental interference will be discussed.

Timing of flowering:

The timing of flowering was assessed by dividing flower development into five identifiable stages. These stages are described in Fig. 2-1 and Fig. 2-2. A brief summary of the progress of flowering is featured in Table 4-10. In general, the males flowered slightly ahead of the females. The chi-square analyses of the differences in flowering timing between the sexes for each day (Table 4-11), show that generally males and females do differ significantly.

Since timing of flowering may be influenced by tree health, the condition of each tree was evaluated during the flowering period. Any tree where beaver damage exceeded 50 percent girdling, the main beam of the trunk was dead, decrepit, or influenced by human pruning activities, or very few catkins

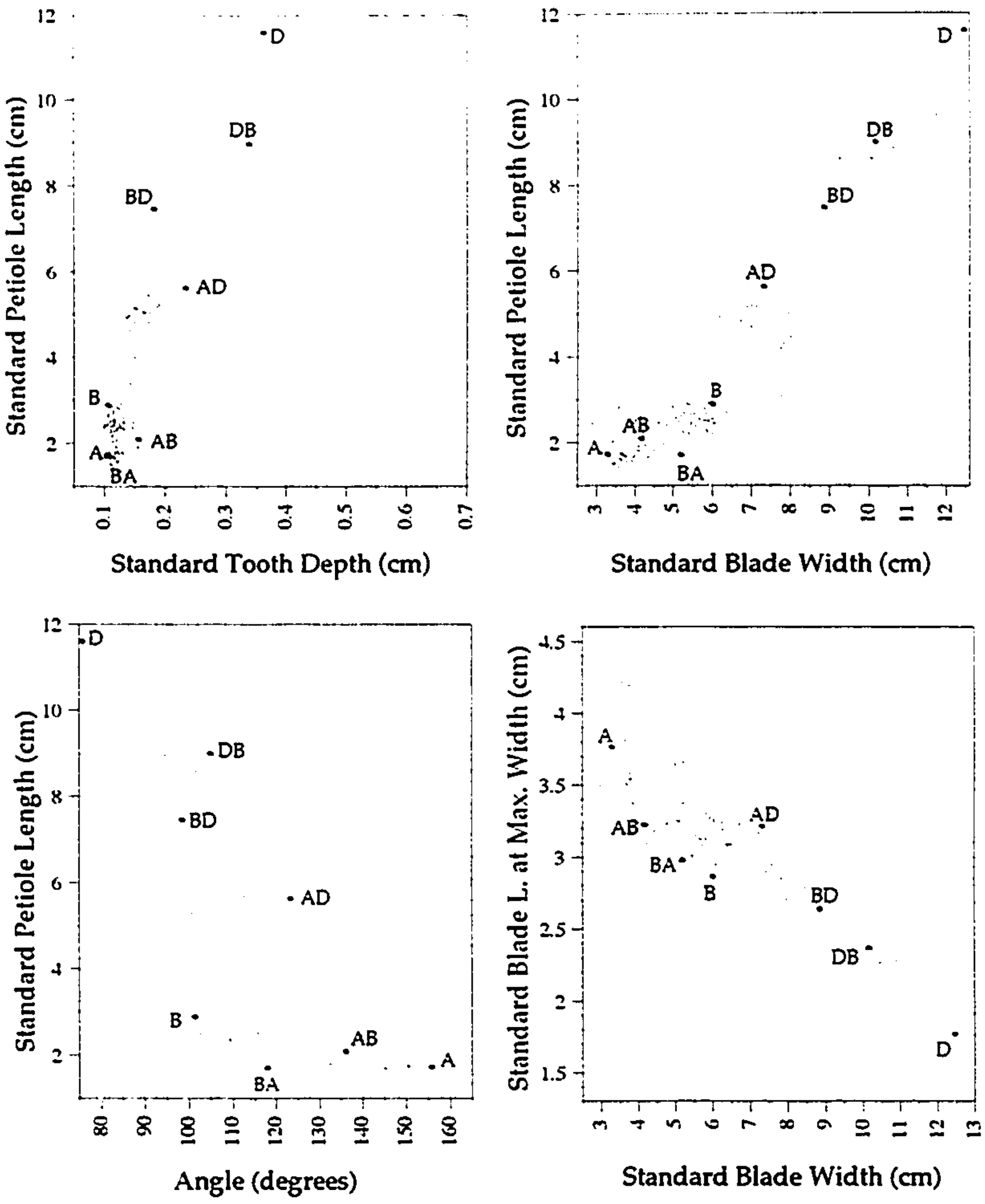


Figure 4-15. Trends in leaf measurements, with the eight individuals chosen to characterize leaf-shape identified (N=391).

Table 4-10. Summary of the number of trees, in each flowering stage, for each observation date. Trees of unknown sex are excluded. Where intermediate codes of 0.5, 1.5, 2.5, or 3.5 were encountered, the number of occurrences were split evenly between the two main categories. Values in the "?" coded column indicate trees with suspicious or missing values. Shaded cells indicate the flowering stage containing the highest number of individuals found on that date (female n=204 and male n=116).

JULIAN		# OF TREES AT EACH FLOWERING STAGE:					
DATE	SEX	0	1	2	3	4	?
DAY122	F	129	69	3	0	0	3
(May 2/95)	M	61	29	17	9	0	0
DAY125	F	104.5	37.5	56	0	0	6
(May 5/95)	M	35.5	37.5	25	11.5	6.5	0
DAY128	F	91	20.5	38	48.5	0	6
(May 8/95)	M	20.5	42	23.5	16	14	0
DAY130	F	70	19	18.5	84.5	0	12
(May 10/95)	M	8	28	32.5	24	20.5	3
DAY133	F	25.5	47.5	13.5	79	25.5	13
(May 13/95)	M	4.5	15.5	35	22	35	4
DAY137	F	6	24.5	31	30	110.5	2
(May 17/95)	M	0	5.5	12	41.5	55	2
DAY139	F	1	5	26	41	131	0
(May 19/95)	M	0	0	7	22	85	2
DAY143	F	0	3	3.5	28	168.5	1
(May 23/95)	M	0	0	0	14	100	2
DAY145	F	0	2	1	18.5	181.5	1
(May 25/95)	M	0	0	0	2	112	2

Table 4-11. Summary of the chi-square evaluations comparing flowering-stage progression in males and females. The number of occurrences of the intermediate codes 0.5, 1.5, 2.5, or 3.5 were split evenly between the two main categories. (female n=204 and male n=116)

Null Hypothesis: The flowering stages of males and females have the same distribution of occurrence.

JULIAN DATE	SEX		FLOWERING STAGES: 0	1	2	3	4	df:	crit. X^2:	calc. X^2:	DECISION
DAY122	F	Obs:	129	69	3	0	0				
		Exp:	120.47	62.14	12.68	5.71	0.00	3	7.81	39.51	REJECT the Null
	M	Obs:	61	29	17	9	0				
		Exp:	69.53	35.86	7.32	3.29	0.00				
DAY125	F	Obs:	104.5	37.5	56	0	0				
		Exp:	88.28	47.29	51.08	7.25	4.10	3	7.81	34.47	REJECT the Null
	M	Obs:	35.5	37.5	25	11.5	6.5				
		Exp:	51.72	27.71	29.92	4.25	2.40				
DAY128	F	Obs:	91	20.5	38	48.5	0				
		Exp:	70.31	39.41	38.78	40.67	8.83	3	7.81	39.51	REJECT the Null
	M	Obs:	20.5	42	23.5	16	14				
		Exp:	41.19	23.09	22.72	23.83	5.17				
DAY130	F	Obs:	70	19	18.5	84.5	0				
		Exp:	49.10	29.59	32.10	68.30	12.90	4	9.49	94.99	REJECT the Null
	M	Obs:	8	28	32.5	24	20.5				
		Exp:	28.90	17.41	18.90	40.20	7.60				
DAY133	F	Obs:	25.5	47.5	13.5	79	25.5				
		Exp:	18.35	46.32	25.57	64.37	36.40	4	9.49	57.45	REJECT the Null
	M	Obs:	4.5	15.5	35	22	35				
		Exp:	11.09	23.29	17.93	37.33	22.36				
DAY137	F	Obs:	6	24.5	31	30	110.5				
		Exp:	3.84	19.18	27.49	45.71	105.79	4	9.49	24.27	REJECT the Null
	M	Obs:	0	5.5	12	41.5	55				
		Exp:	2.16	10.82	15.51	25.79	59.71				
DAY139	F	Obs:	1	5	26	41	131				
		Exp:	0.64	3.21	21.17	40.42	138.57	3	7.81	7.04	FAIL TO REJECT
	M	Obs:	0	0	7	22	85				
		Exp:	0.36	1.79	11.83	22.58	77.43				
DAY143	F	Obs:	0	3	3.5	28	168.5				
		Exp:	0.00	1.92	2.24	26.90	171.94	2	5.99	2.28	FAIL TO REJECT
	M	Obs:	0	0	0	14	100				
		Exp:	0.00	1.08	1.26	15.10	96.56				
DAY145	F	Obs:	0	2	1	18.5	181.5				
		Exp:	0.00	1.28	0.64	13.13	187.95	1	3.84	6.73	REJECT the Null
	M	Obs:	0	0	0	2	112				
		Exp:	0.00	0.72	0.36	7.37	105.55				

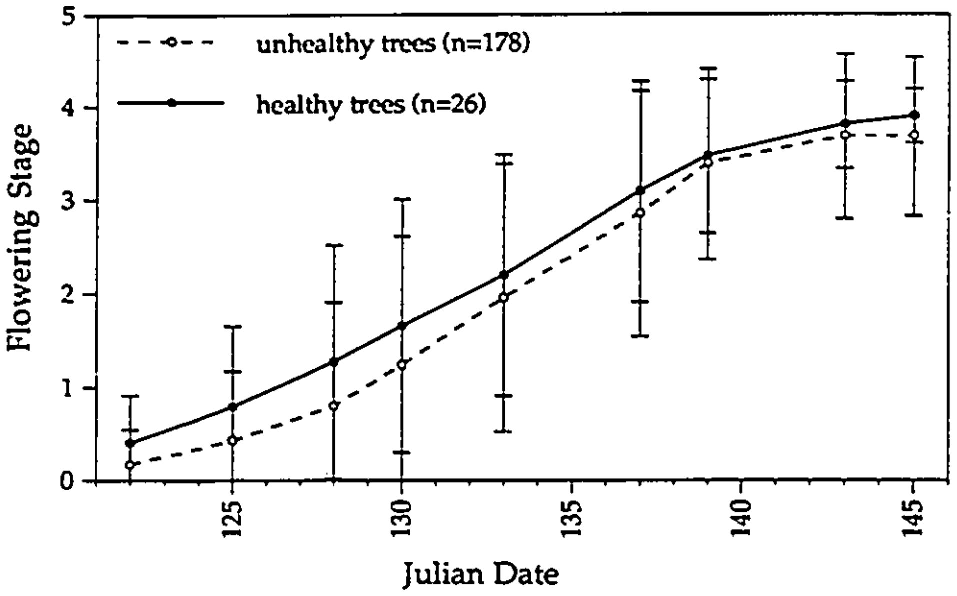
were observed, was considered unhealthy in later analyses. In general, it was found that healthy individuals tended to flower slightly earlier than unhealthy ones (Fig. 4-16). In these individuals it is possible that poor health has resulted in delayed flowering, or alternatively, that late flowering is a characteristic which has led to or is associated with a generally weaker genotype.

A series of plots have been generated to investigate other factors with potential for influencing flowering trends. When the averaged flowering stages of all individuals are plotted, a gradual slope with wide standard deviation is produced (Fig. 4-17). Sex-related differences are responsible for part of this wide range in standard deviation (Fig. 4-18), since males tend to flower earlier than females. When the sexes are further subdivided according to species, variability is further restricted (Fig 4-19 and Fig. 4-20). In summary, the trends and variability in this population's flowering phenology supports the use of such patterns in clone delineation as long as those subject to impaired health are not incorporated.

Timing of leaf-flush:

Since the sexes differ in the timing of flowering, it was thought that the progression of leaf flush might follow a similar trend. Table 4-12 summarizes the general leaf-flush trends observed in the sexes. The chi-square evaluations of the differences between the sexes (Table 4-13) show that females flush earlier but that males rapidly catch up. Since health could influence leaf-flushing, the trends were compared according to health (Fig. 4-21 and Fig. 4-22), and it was shown that poor health coincides with delayed leaf-flushing. As was the case for flowering trends, poor health may have caused slower leaf-flushing, or alternatively individuals with slower flushing

a) Female flowering trends:



b) Male flowering trends:

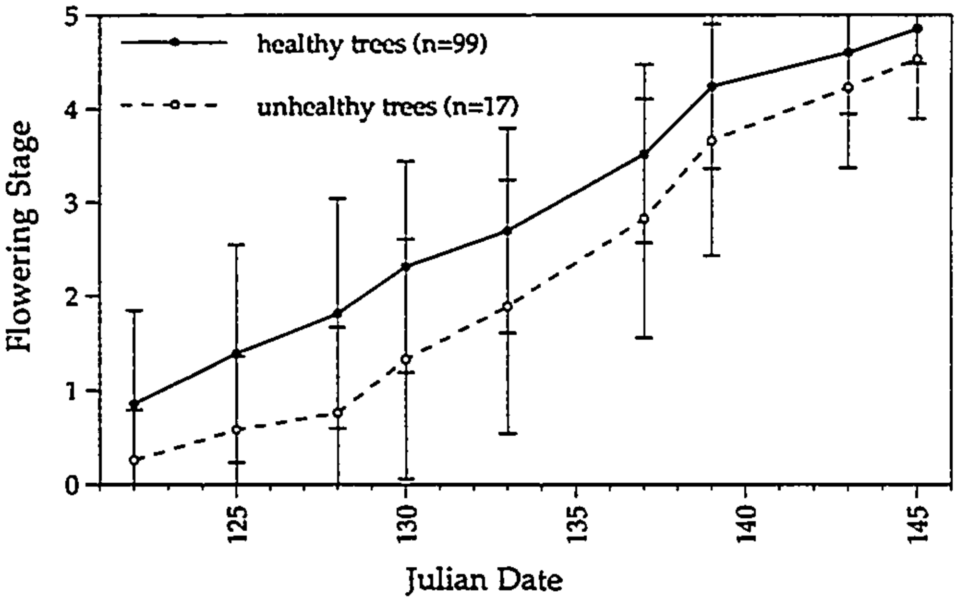


Figure 4-16. Flowering trends in healthy versus unhealthy, male and female trees. Each error bar indicates one standard deviation.

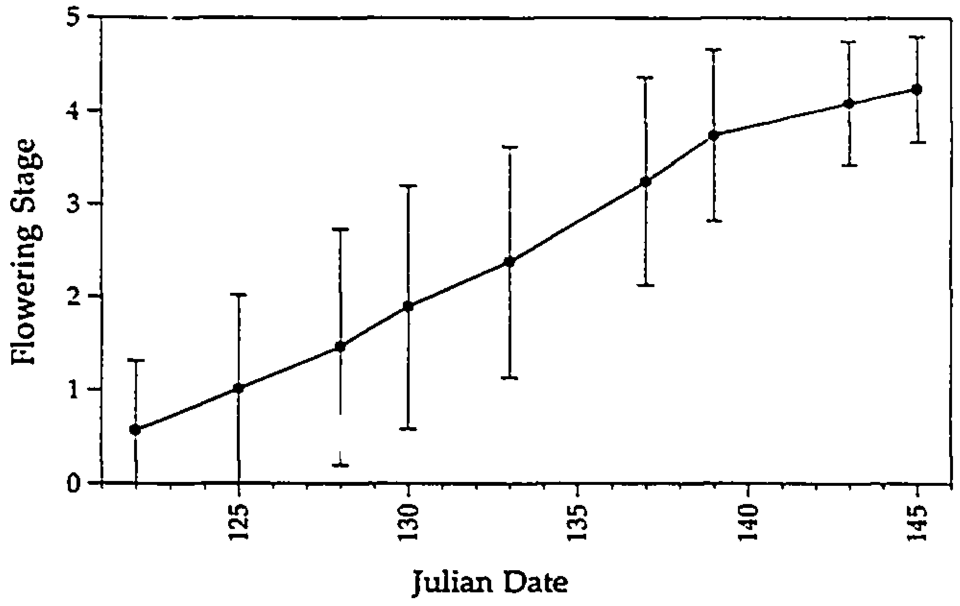


Figure 4-17. Flowering trends in all healthy trees (N=277). Each error bar indicates one standard deviation.

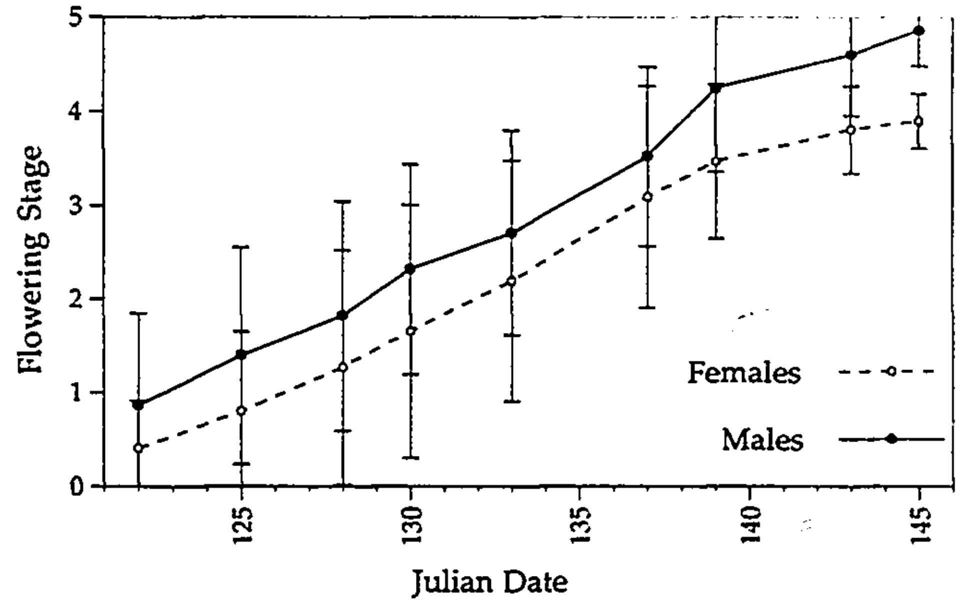
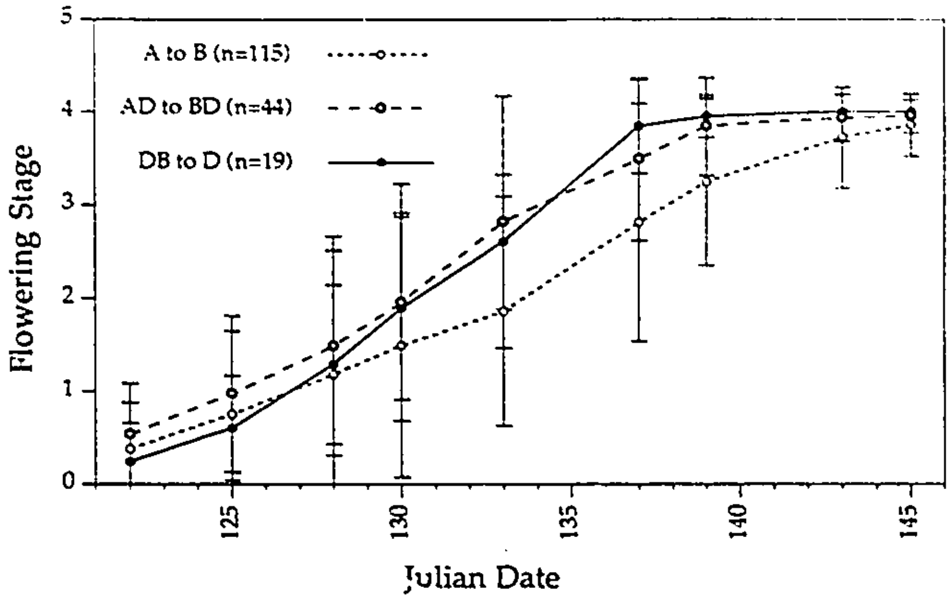


Figure 4-18. Flowering trends in healthy males (n=99) versus females (n=178). Each error bar indicates one standard deviation.

a) Healthy Females:



b) Healthy Males:

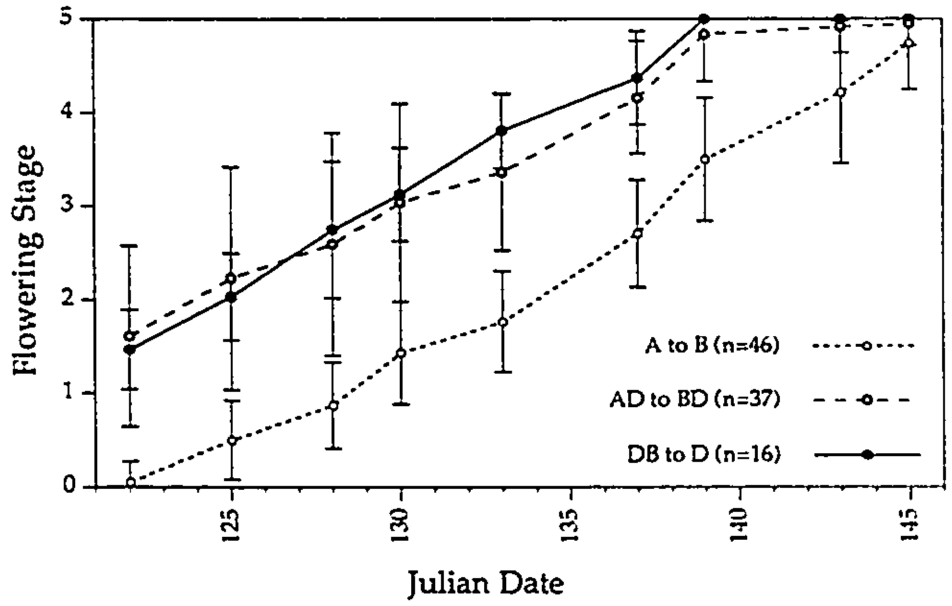
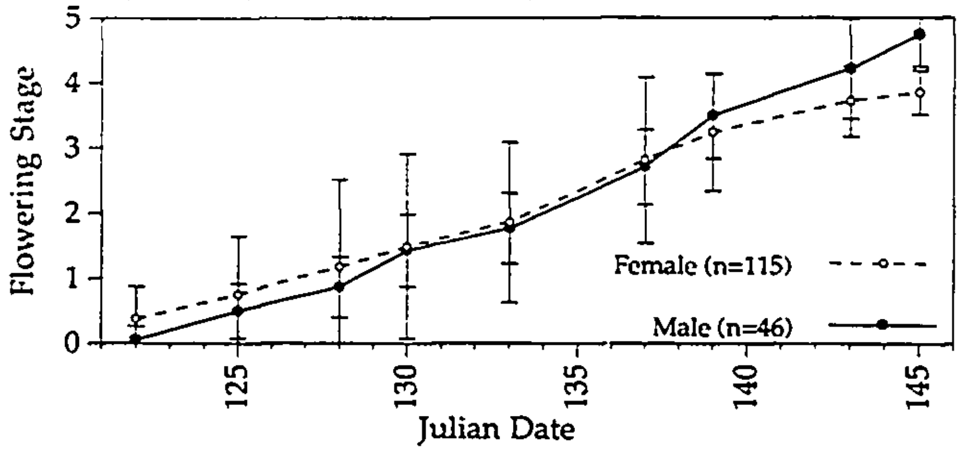
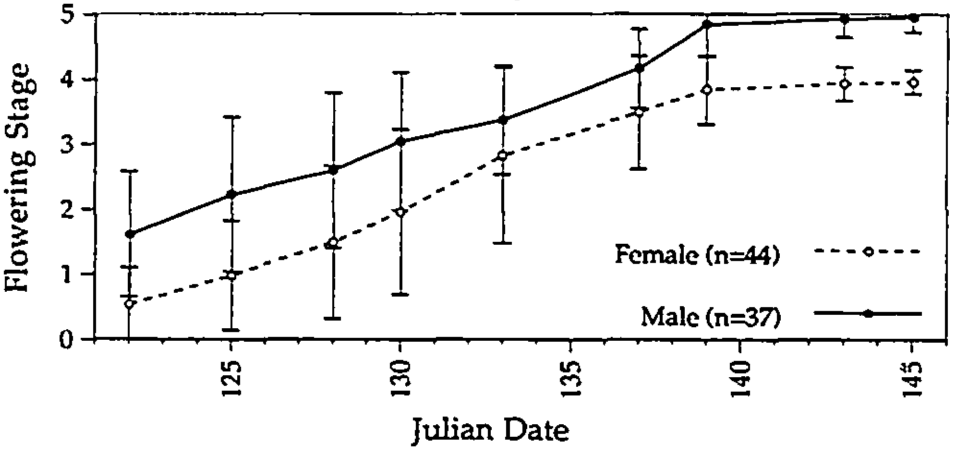


Figure 4-19. Flowering trends in healthy a) female, and b) male trees of the three species-related categories; A to B (section Tacamahaca), AD to BD (intersectional hybrids), and DB to D (section Aigeiros). Each error bar indicates one standard deviation.

a) A to B (section Tacamahaca)



b) AD to BD (intersectional hybrids)



c) DB to D (section Aigeiros)

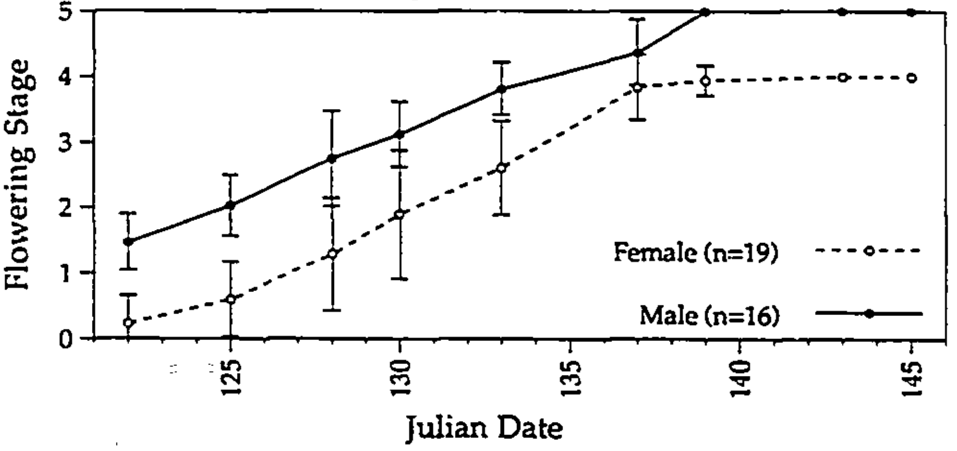


Figure 4-20. Flowering trends in healthy males versus females, for each species-related category; a) A to B (section Tacamahaca), b) DB to D (section Aigeiros), c) AD to BD (intersectional hybrids).

Table 4-12. Summary of the number of trees, in each leaf-flushing stage, for each observation date. Trees of unknown sex are excluded. Shaded cells indicate the flushing stage containing the highest number of individuals found on that date. (female n=183, male n=105)

JULIAN		# OF TREES AT EACH LEAF-FLUSHING STAGE:			
DATE:	SEX:	0	0.5	1	2
DAY130	F	94	89	0	0
(May 10/95)	M	71	34	0	0
DAY133	F	41	92	50	0
(May 13/95)	M	33	70	2	0
DAY137	F	1	56	51	75
(May 17/95)	M	2	34	66	3
DAY139	F	0	39	21	123
(May 19/95)	M	0	23	18	64
DAY143	F	0	7	34	142
(May 23/95)	M	0	3	25	77
DAY145	F	0	1	18	164
(May 25/95)	M	0	1	13	91

Table 4-13. Summary of the chi-square evaluation comparing leaf-flush stage progression in males (n=105) and females (n=183).

Null Hypothesis: The leaf-flushing stages of males and females have the same distribution of occurrence.

JULIAN DATE	SEX		LEAF-FLUSHING STAGES: 0	0.5	1	2	df:	crit. X^2:	calc. X^2:	DECISION
DAY130	F	Obs:	94	89	0	0				
		Exp:	104.84	78.16	0.00	0.00	1	3.84	7.20	REJECT the Null
	M	Obs:	71	34	0	0				
		Exp:	60.16	44.84	0.00	0.00				
DAY133	F	Obs:	41	92	50	0				
		Exp:	47.02	102.94	33.04	0.00	2	5.99	29.18	REJECT the Null
	M	Obs:	33	70	2	0				
		Exp:	26.98	59.06	18.96	0.00				
DAY137	F	Obs:	1	56	51	75				
		Exp:	1.91	57.19	74.34	49.56	3	7.81	57.16	REJECT the Null
	M	Obs:	2	34	66	3				
		Exp:	1.09	32.81	42.66	28.44				
DAY139	F	Obs:	0	39	21	123				
		Exp:	0.00	39.40	24.78	118.82	2	5.99	2.00	FAIL TO REJECT
	M	Obs:	0	23	18	64				
		Exp:	0.00	22.60	14.22	68.18				
DAY143	F	Obs:	0	7	34	142				
		Exp:	0.00	6.35	37.49	139.16	2	5.99	1.23	FAIL TO REJECT
	M	Obs:	0	3	25	77				
		Exp:	0.00	3.65	21.51	79.84				
DAY145	F	Obs:	0	1	18	164				
		Exp:	0.00	1.27	19.70	162.03	2	5.99	0.63	FAIL TO REJECT
	M	Obs:	0	1	13	91				
		Exp:	0.00	0.73	11.30	92.97				

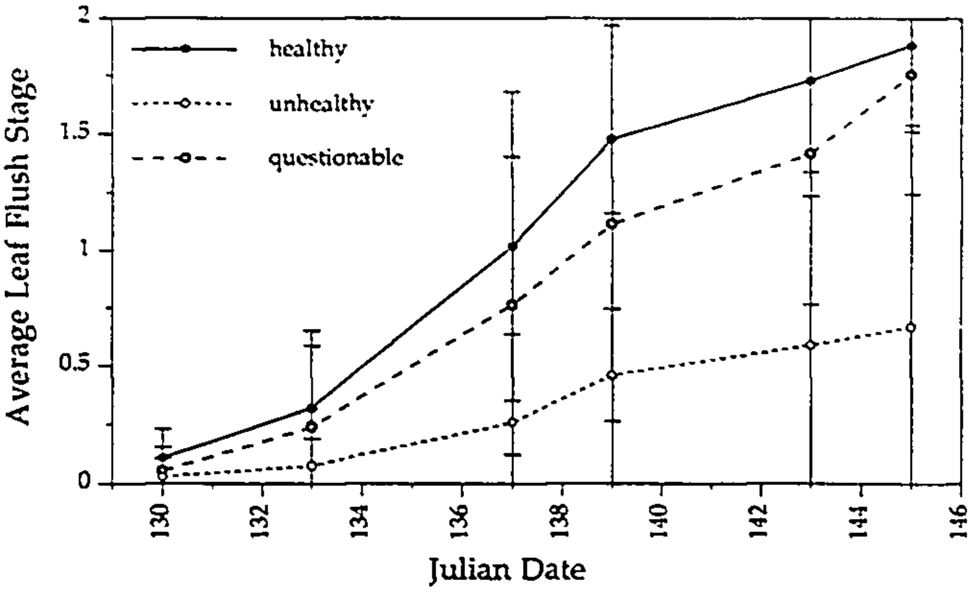


Figure 4-21. Timing of bud flush and leaf expansion in trees of good (n=315), poor (n=37), and questionable health (n=39). Error bars indicate one standard deviation.

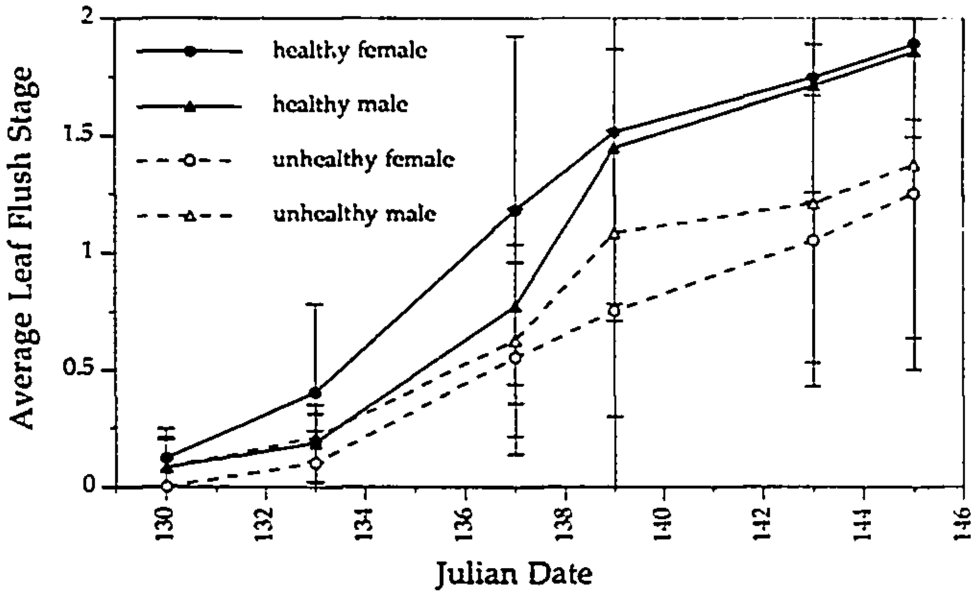


Figure 4-22. Timing of bud flush and leaf expansion in healthy and unhealthy males (n=105, n=6) and females (n=183, n=5). Error bars indicate one standard deviation.

may have been otherwise disadvantaged resulting in poor health. To avoid the generation of artifact, unhealthy individuals were removed from further analyses.

To trace differences among the species, Fig. 4-23 depicts leaf-flush trends according to three species-related categories of leaf shape. The trends are obvious, with members of section *Tacamahaca* flushing first, followed by the intersectional hybrids, and then by members of section *Aigeiros*. Fig. 4-24 shows that little of the variance within the species categories is due to differences in sex.

Maturity is another factor which might influence this type of phenology. Since trunk circumference provides an index of tree size and so roughly approximates maturity, three general categories were plotted for each species category to detect associated differences (Fig. 4-25). Since flushing differences between the size categories were small, it was decided that maturity as judged by trunk-size does not have a significant influence over flushing phenology. In summary, the trends thus presented serve to support the use of leaf-flushing phenology in clone delineation, granted that impaired health is not permitted to contribute.

Timing of leaf-senescence:

Trends in the timing of autumn leaf-senescence were evaluated similarly to those in flowering and leaf-flushing. The effect of health on senescence is plotted in Fig. 4-26. Unhealthy individuals tended to begin scenescing earlier and take longer to finish. The leaf-senescence trends of healthy males, females, and trees of unknown sex appeared not to differ significantly (Fig. 4-27). Species-related differences were obvious (Fig. 4-28), with the members of

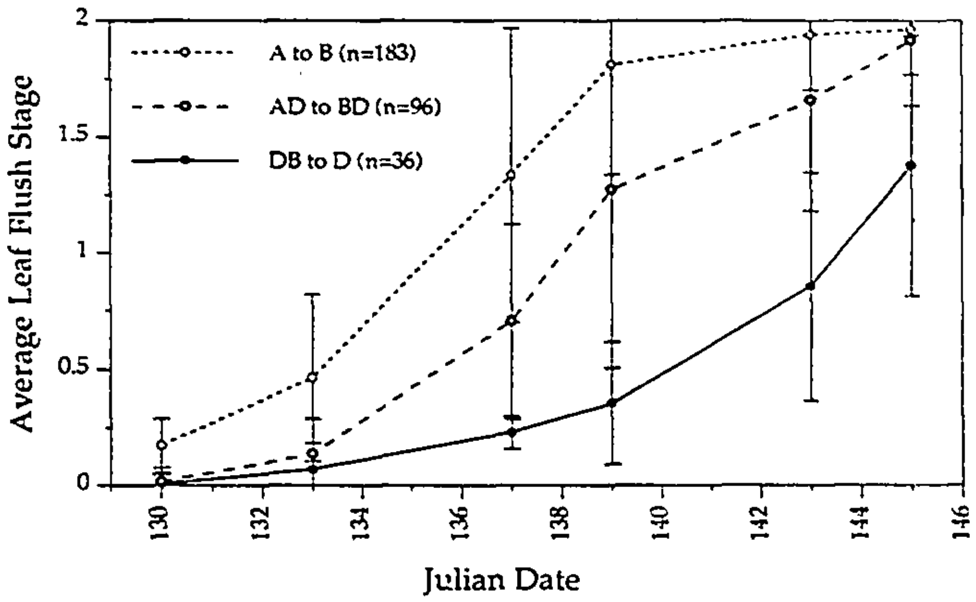
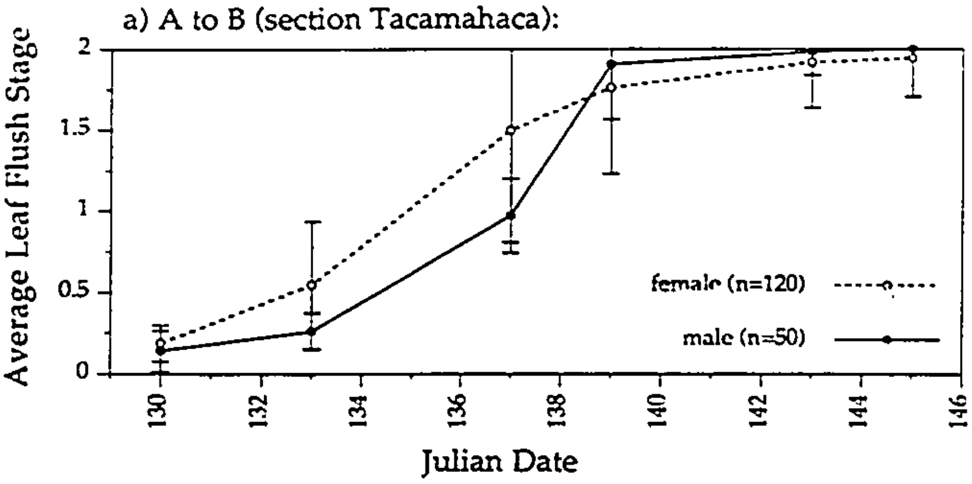
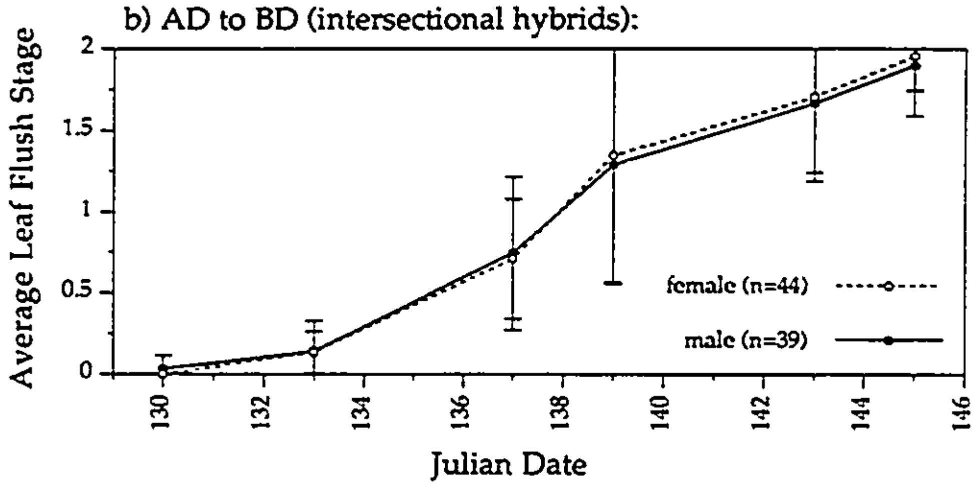


Figure 4-23. Trends in the timing of leaf-flush in healthy trees of the three species-related groups;
A to B (section Tacamahaca), AD to BD (intersectional hybrid), DB to D (section Aigeiros).
Error bars indicate one standard deviation.

a) A to B (section Tacamahaca):



b) AD to BD (intersectional hybrids):



c) DB to D (section Aigeiros):

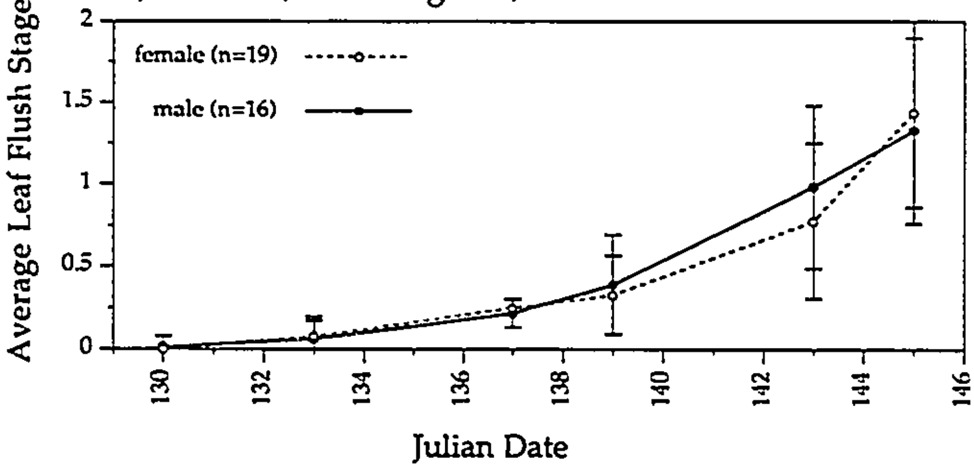
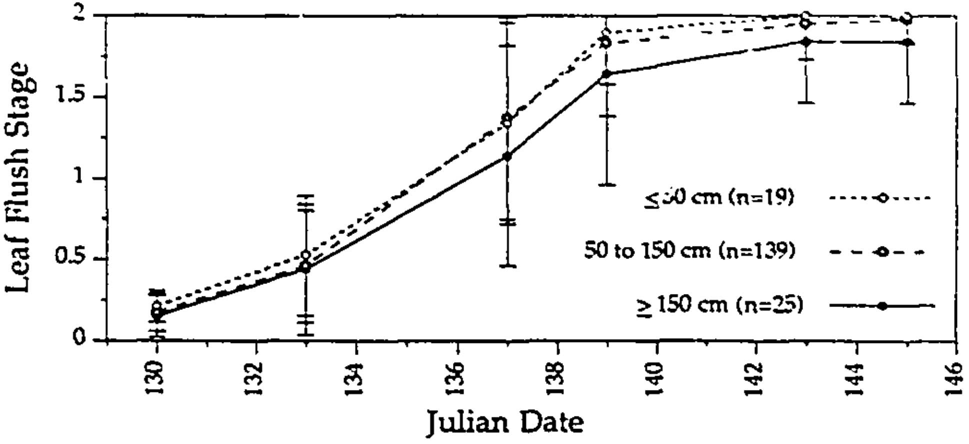
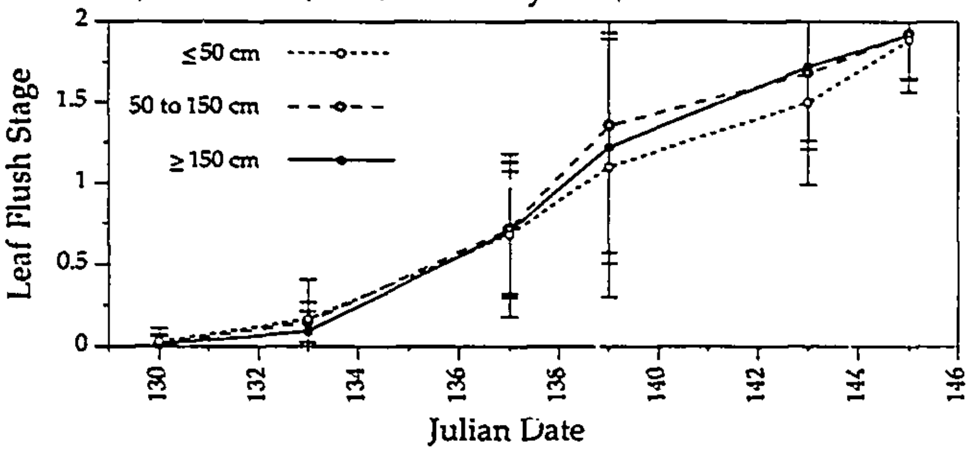


Figure 4-24. Male versus female trends in leaf-flush for healthy trees in the species- related categories. Error bars signify one standard deviation.

a) A to B (section Tacamahaca):



b) AD to BD (intersectional hybrids).



c) DB to D (section Aigeiros):

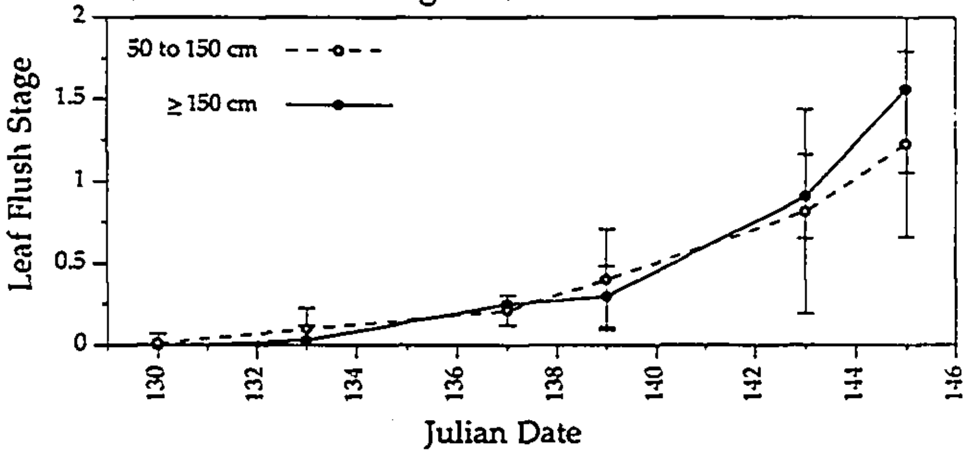


Figure 4-25. Comparing leaf-flushing phenology between three trunk circumference classes for healthy trees of each species category. Error bars signify one standard deviation.

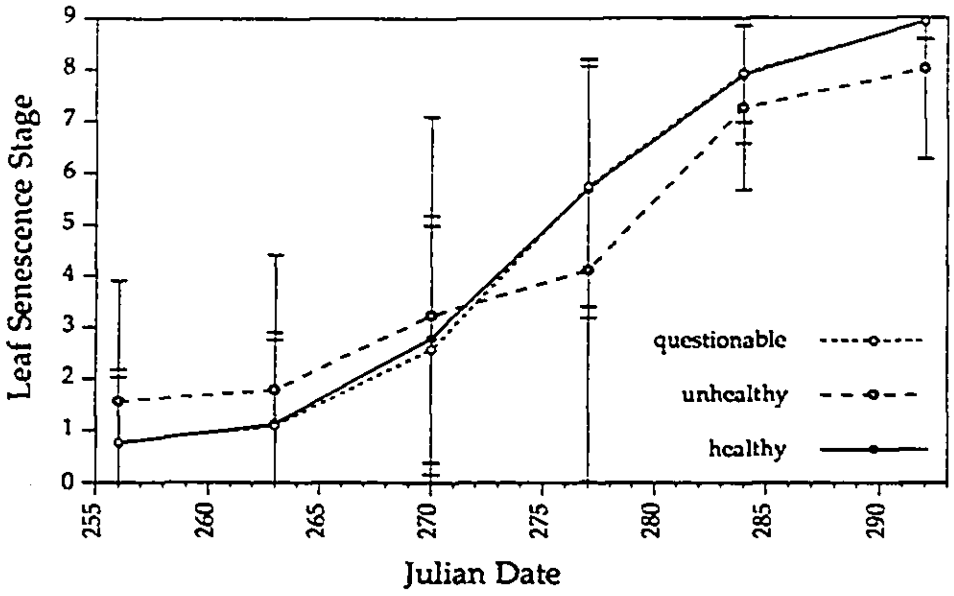


Figure 4-26. Timing of leaf senescence in trees of good (n=300), poor (n=9), and questionable health (n=46). Error bars indicate standard deviations.

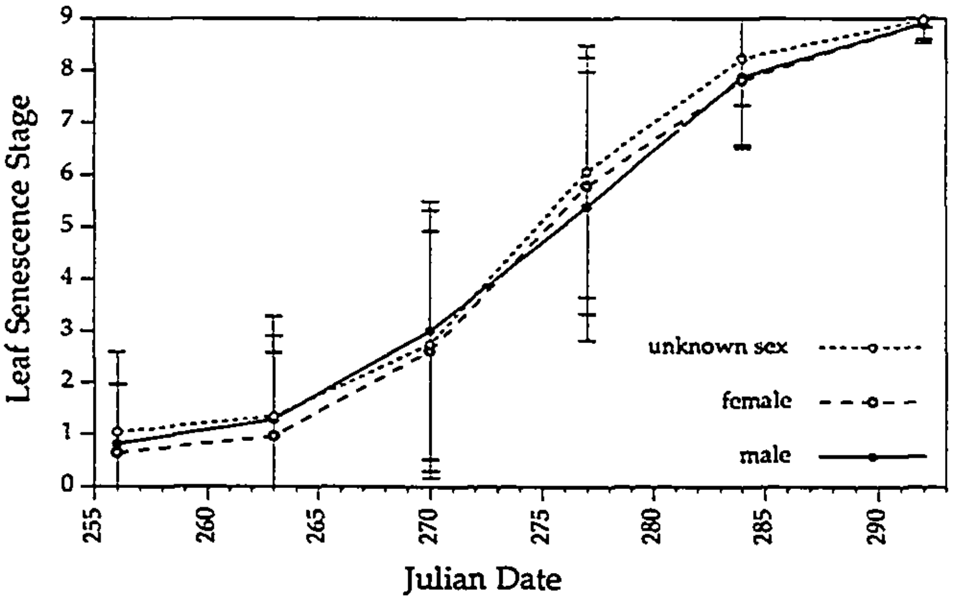


Figure 4-27. Timing of leaf senescence in healthy males (n=97), females (n=179), and trees of unknown sex (n=24). Error bars indicate standard deviations.

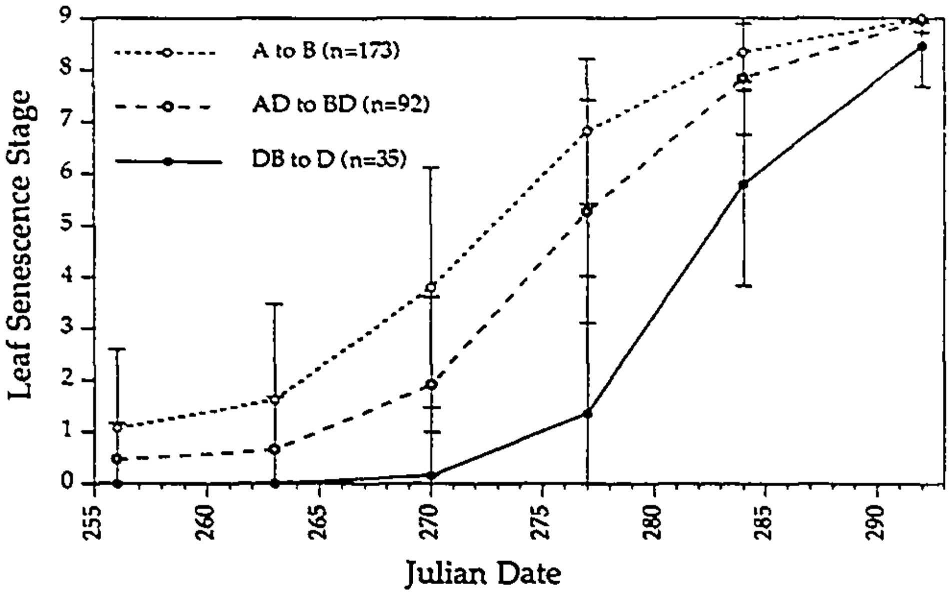


Figure 4-28. Timing of leaf senescence in healthy trees of the three species-related categories.
Error bars indicate standard deviations.

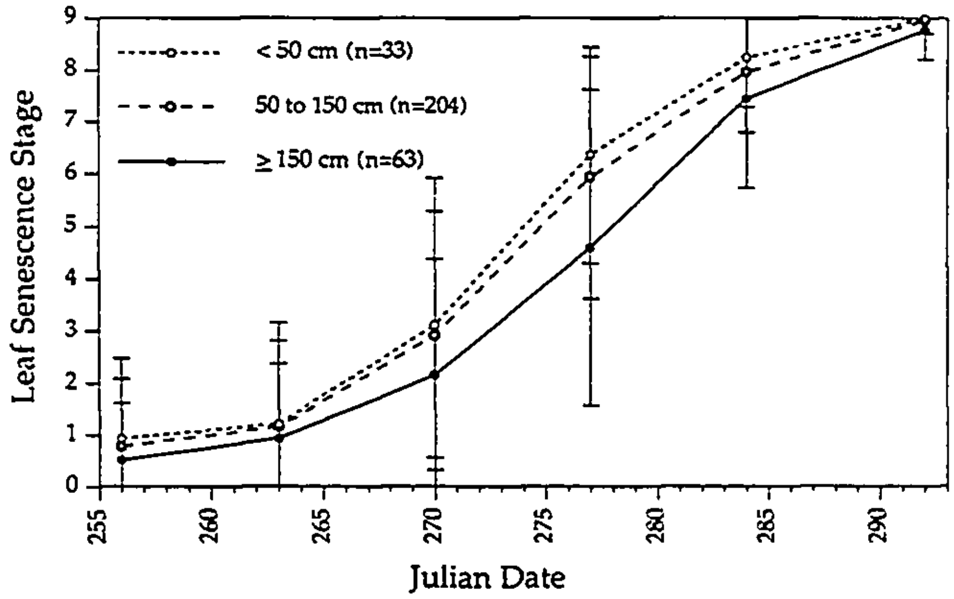


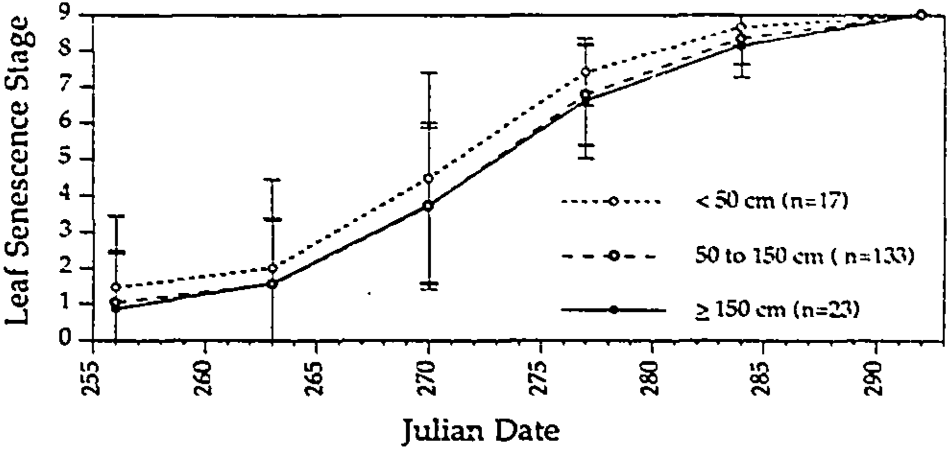
Figure 4-29. Timing of leaf senescence in healthy trees of three classes of trunk circumference.
Error bars indicate standard deviations.

section *Tacamahaca* starting to senesce first, followed by the interspecific hybrids, and then the members of section *Aigeiros*. In the three trunk-circumference defined maturity classes (Fig. 4-29), the larger trees tended to senesce slightly later than the smaller ones. This trend was weaker when each species-related group was separately divided into the three circumference categories (Fig. 4-30).

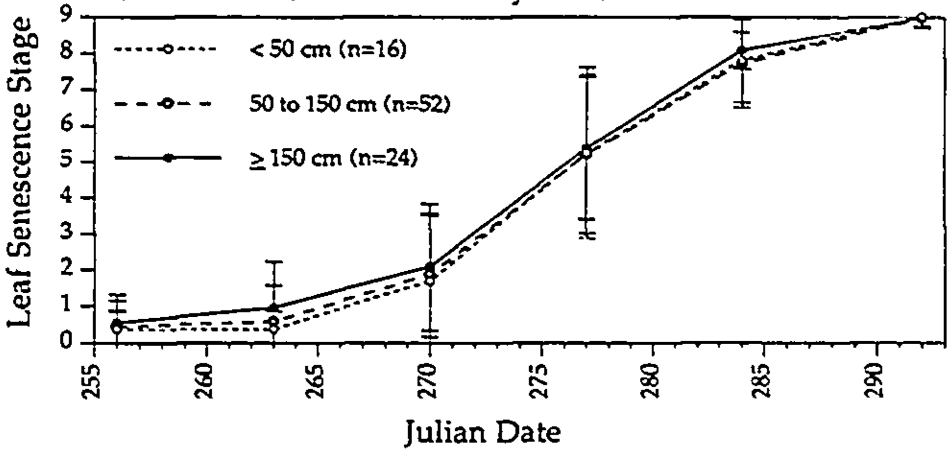
Timing of leaf-drop:

The trends in leaf-abscission were graphically illustrated in the same manner as for leaf-senescence. To avoid variation in leaf-drop which could be caused by poor health (Fig. 4-31), it was decided to only consider healthy individuals. Fig. 4-32 shows the variation in leaf-drop associated with differences in sex, and Fig. 4-33 depicts trends according to species. The trees of unknown sex tend to initiate leaf-drop sooner than those of known sex. Many of these unsexed trees were too young to flower, so it is possible that accelerated leaf-drop is associated with immaturity. Trunk circumference offers another estimation of maturity-related effects. When leaf-drop trends are divided into three circumference categories, their pattern suggests that the smaller the tree, the faster it begins and completes autumn leaf-drop (Fig. 4-34). To be sure that this effect is not a reflection of a skewed size distribution between species, the circumference categories in each species group were also viewed separately (Fig. 4-35). Here, the same trends related to circumference size appear to varying degrees. These illustrations advocate caution when interpreting leaf-drop as a genetically conserved character, especially when comparing trees of widely differing sizes.

a) A to B (section Tacamahaca):



b) AD to BD (intersectional hybrids):



c) DB to D (section Aigeiros):

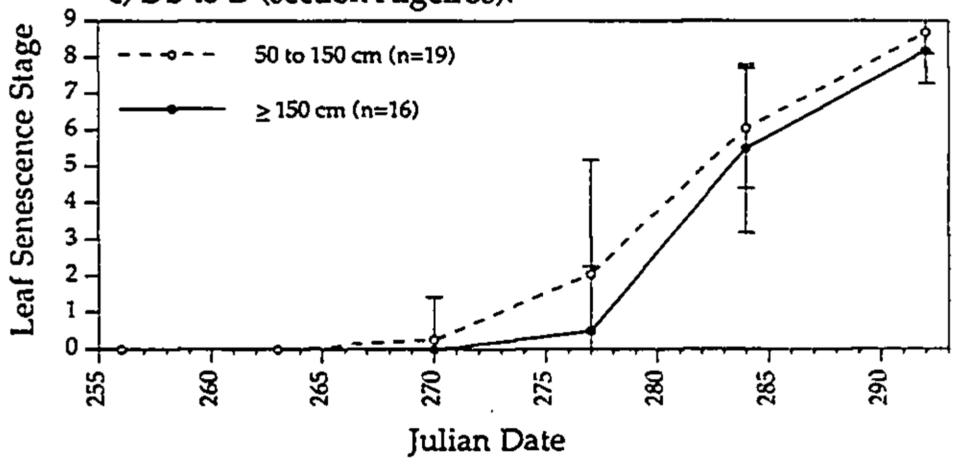


Figure 4-30. Comparing the timing of leaf-senescence in three trunk circumference classes for healthy trees of three species-related categories. Error bars signify standard deviations.

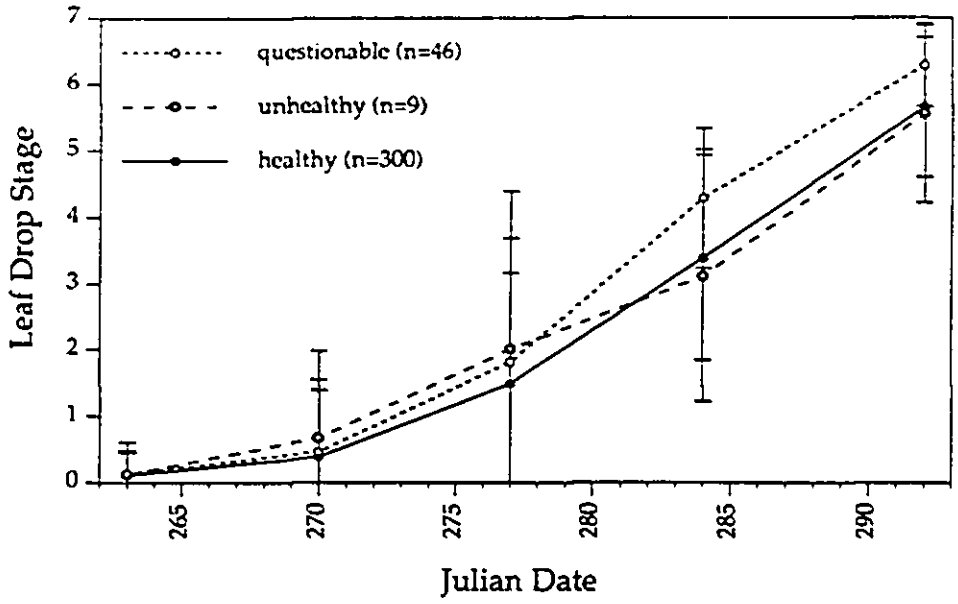


Figure 4.31. The timing of leaf drop in the three categories of tree health.
Each error bar indicates one standard deviation.

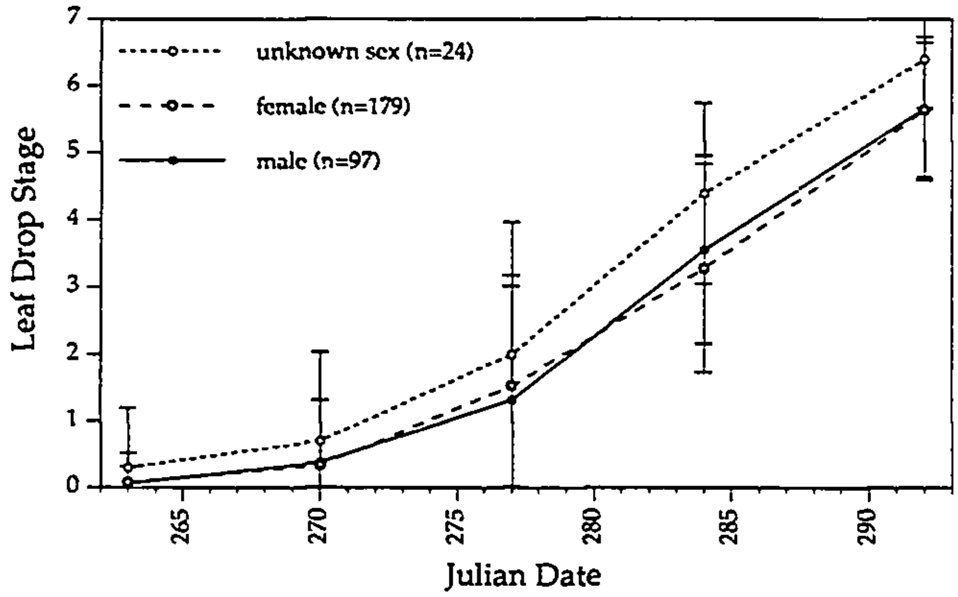


Figure 4.32. The timing of leaf drop in healthy trees of the sex categories.
Each error bar indicates one standard deviation.

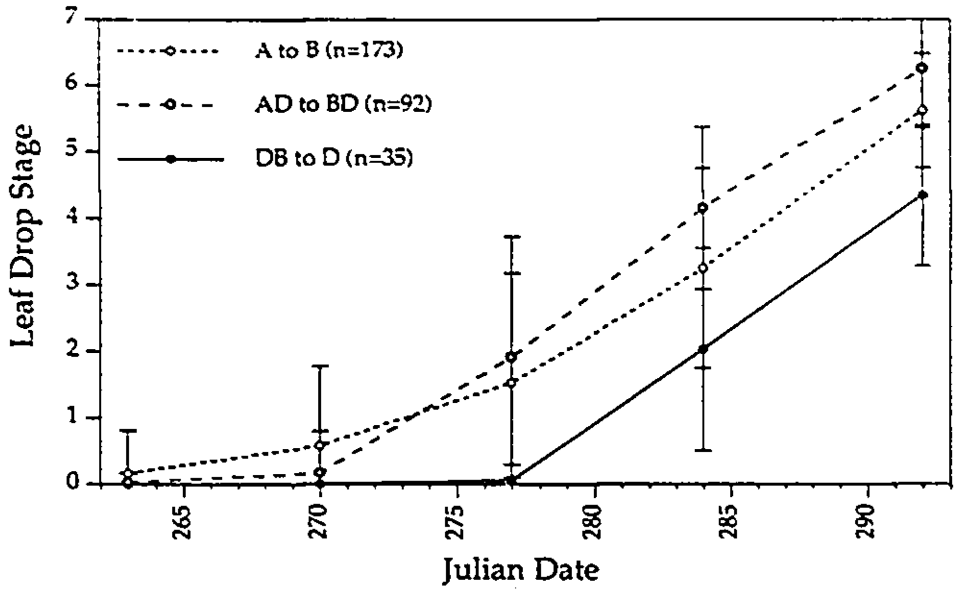


Figure 4-33. The timing of leaf drop in healthy trees of three species- related categories.
Each error bar indicates one standard deviation.

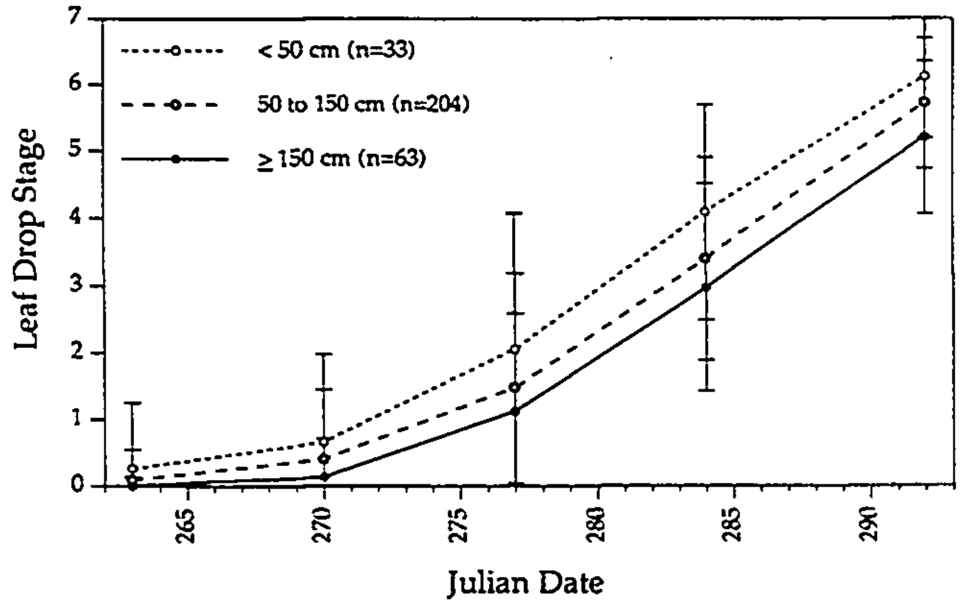
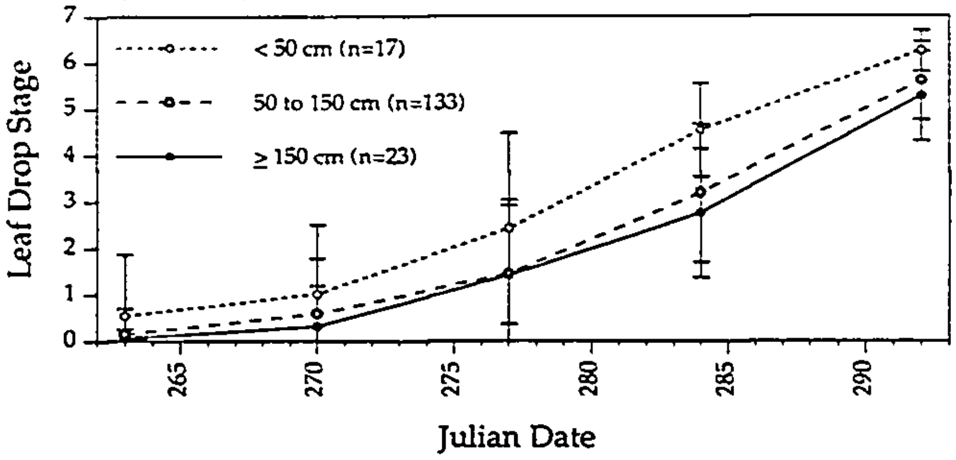
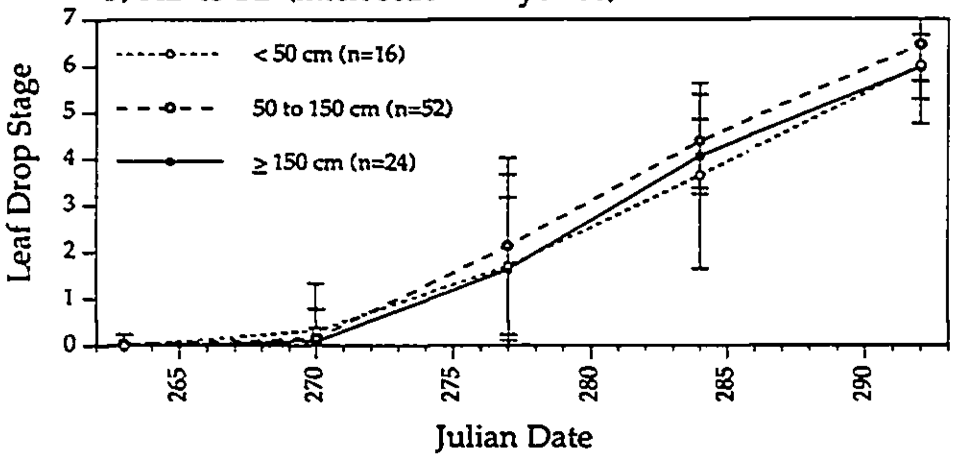


Figure 4-34. The timing of leaf drop in healthy trees of three classes of trunk circumference.
Each error bar indicates one standard deviation.

a) A to B (section Tacamahaca):



b) AD to BD (intersection al hybrids):



c) DB to D (section Aigeiros):

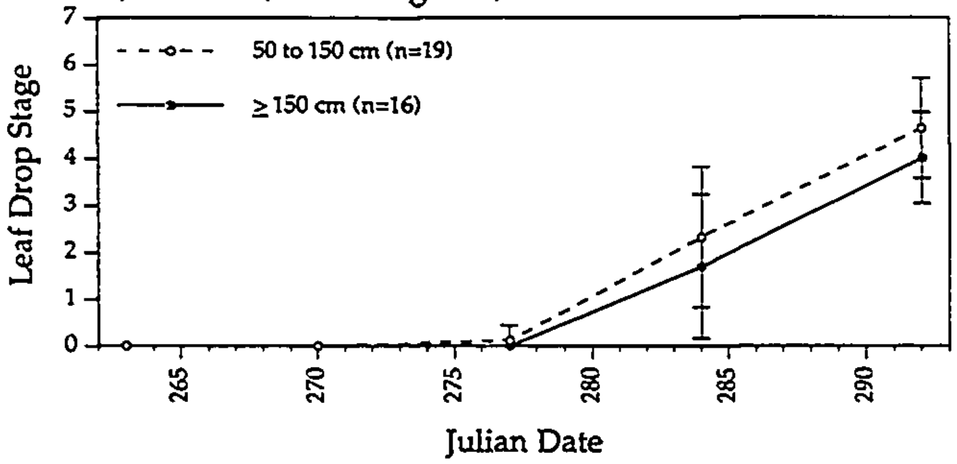


Figure 4-35. The timing of leaf drop in healthy trees of the three trunk circumference classes in the species-related categories. Each error bar indicates one standard deviation.

Occurrence of branch sacrifice:

In addition to autumn observations of leaf-senescence and leaf-abscission, the occurrence of branch sacrifice was also surveyed. To gauge this character's variability and trends, its occurrence in relation to sex, species, and trunk circumference was investigated (Fig. 4-36). The chi-square analyses of these distributions are presented in Table 4-14, Table 4-15, and Table 4-16. In summary, while the sexes did not differ in their occurrence of branch sacrifice, the species and circumference categories did. Species-related patterns suggest a genetic predisposition towards branch sacrifice in *P. deltoides*-related species categories. These species-based trends are also reflected in those of the circumference categories since large *P. deltoides*-type trees are common. Another explanation is that in general, larger more mature trees are more likely to demonstrate branch sacrifice than younger ones. Due to this complexity, cautious use of branch sacrifice as a genetically conserved character is recommended, especially when comparing trees of different sizes. For this reason, branch sacrifice was not used to delineate clones here.

4.1.3 Indirectly clonally-conserved characters:

In addition to the characteristics of sex, species, and timing of flowering, leaf flush and leaf senescence, a selection of less heritable characteristics are available to assist investigations of clonality. Among these, closely spaced trunks, trunk architecture, and abundance of mite-galls are evaluated here to decide their utility for aspects of clone delineation.

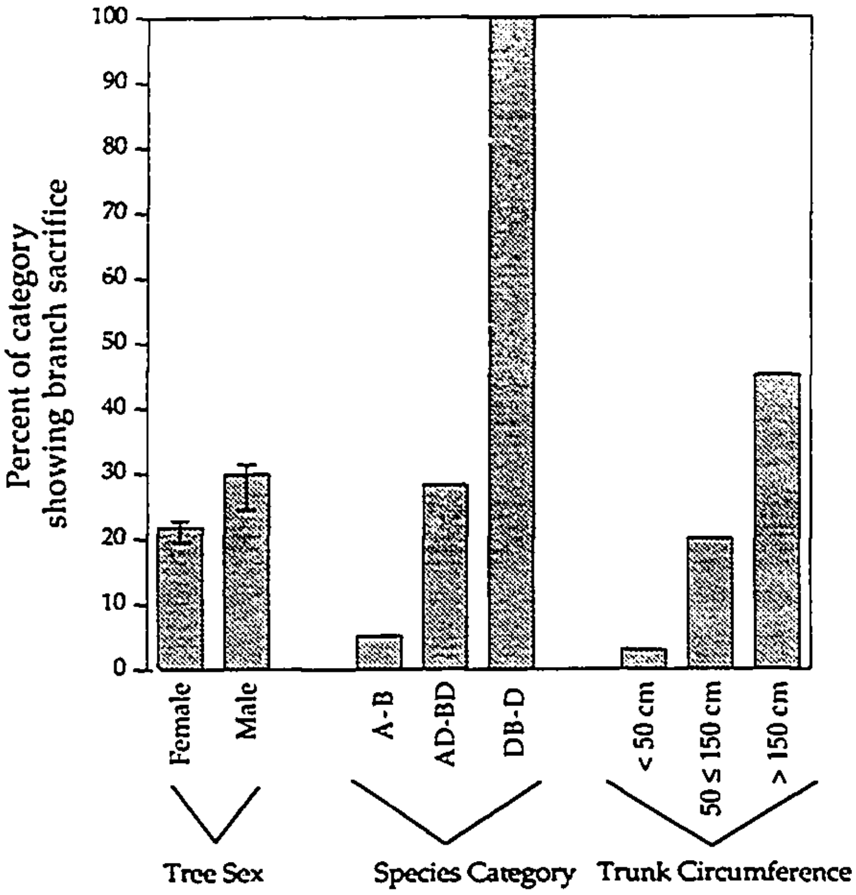


Figure 4-36. Differences in the occurrence of branch sacrifice among healthy individuals (N=300) according to sex, species, and trunk circumference categories (females: n=179, males: n=97, unknown sex: n=24, A-B: n=173, AD-BD: n=92, DB-D: n=35, <50 cm: n=33, 50≤150 cm: n= 205, >150 cm: n= 62). The error bars indicate the maximum potential for influence by the unknown sex category.

Table 4-14. Using the X^2 Test of Independence: Do males and females differ in their occurrence of branch sacrifice?

(Contingency Table:)

		Branch Sacrifice: Yes:	Branch Sacrifice: No:	Totals:
Female Trees:	Obs:	39	140	179
	Exp:	44.10	134.90	179
Male Trees:	Obs:	29	68	97
	Exp:	23.90	73.10	97
Column Totals:		68	208	276

Null Hypothesis: Males and females have the same occurrence of branch sacrifice.

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 2.2267$

df = 1 $\therefore$ critical X^2 value = 3.84 (α=0.05)

Since $2.2267 < 3.84$ $\therefore$ fail to reject the Null Hypothesis

Conclusion: Males and females do not differ significantly in their occurrence of branch sacrifice.

Table 4.15 Using the X^2 Test of Independence: Do members of the three species categories; AA to BB (section *Tacamahaca*), AD to BD (interspecific hybrids), and DB to DD (section *Aigeiros*), differ in their occurrences of branch sacrifice?

(Contingency Table:)

		Branch Sacrifice:		
		Yes:	No:	Totals:
A to B:	Obs:	9	164	173
	Exp:	40.4	132.6	173
AD to BD:	Obs:	26	66	92
	Exp:	21.5	70.5	92
DB to D:	Obs:	35	0	35
	Exp:	8.2	26.8	35
Column Totals:		70	230	300

Null Hypothesis: Members of the three species-related categories have the same occurrence of branch sacrifice.

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 148.04$

df = 2 $\therefore$ critical X^2 value = 5.99 (α=0.05)

Since 148.04 >> 5.99 $\therefore$ Reject the Null Hypothesis

Conclusion: The members of the three species-related categories differ significantly in their occurrences of branch sacrifice.
-trees in the *Tacamahaca* category had less, and in the *Aigeiros* category had more branch sacrifice than expected

Table 4-16. Using the X^2 Test of Independence: Do members of the three trunk circumference categories; < 50 cm, 50 ≤ 150 cm, and > 150 cm, differ in their occurrences of branch sacrifice?

(Contingency Table:)

		Branch Sacrifice:		
		Yes:	No:	Totals:
≤ 50 cm:	Obs:	1	32	33
	Exp:	7.7	25.3	33
50 ≤ 150 cm:	Obs:	41	164	205
	Exp:	47.8	157.2	205
≥ 150 cm:	Obs:	28	34	62
	Exp:	14.5	47.5	62
	Column Totals:	70	230	300

Null Hypothesis: Members of all three trunk circumference-categories have the same occurrence of branch sacrifice.

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 25.2715$

df = 2 $\therefore$ critical X^2 value = 5.99 (α=0.05)

Since 25.2715 > 5.99 $\therefore$ Reject the Null Hypothesis

Conclusion: The members of these circumference-categories do differ significantly in their occurrences of branch sacrifice.
-large C.B.H. trunks also showed the most branch sacrifice

Closely spaced trunks:

Closely spaced trunks were common in the research population. A total of 102 trunks out of the 390 surveyed, either had abutments with neighboring trunks or were separated by less than 5 cm at the base of their trunks. Table 4-17 summarizes the number of trunks found in each closely spaced group. The sexes and species-compositions of the trunks in each group bear close resemblance to each other in all cases (Table 4-18 and Table 4-19). It is improbable that such trunks, being of such close spacing and similarity, could be of unrelated origin. It is more likely that they are multi-stemmed individuals or very closely spaced ramets. In either case, these trunks contribute to the clonal character of the population.

Trunk architecture:

The designation of trunk architecture summarizes the numerous characters related to branching form. It is thought that tendencies in trunk and branching configuration are tied to species-related differences. To clarify the relationship of growth form to species composition, a chi-square analysis was conducted (Table 4-20). Trees of section *Aigeiros* were found to have a strong tendency toward gnarled trunk architecture. In fact, every large tree of the *P. deltoides* group was attributed gnarled-form. Thus, trunk architecture might be defined at the species level. Trends in architecture were also found to differ according to trunk size (Table 4-21). Small trunks were rarely, judged to be of gnarled form. Since the expression of trunk architecture is complicated by age and size factors, this characteristic is of limited use for clone delineation since it cannot be applied indiscriminately. Added to the subjectivity of classifying the trait, and its redundancy with species-type, trunk architecture will not be utilized further in this investigation.

Table 4-17. Summary of the number of trunks constituting closely-spaced groups (abutted or separated by less than 5 cm at their bases).

# of trunks / group:	# of groups:
2	35
3	9
5	1

Table 4-18. Summary of sex comparisons in closely spaced groups.

Comparison of tree sex in the closely spaced groups:	Proportion of the groups:
Same (exact match)	87%
Unknown (one or more trunks of unknown sex)	13%
Different (male and female trunks in same group)	0%

Table 4-19. Summary of species-category comparisons in closely spaced groups.

Comparison of tree species-category in the closely spaced groups:	Proportion of the groups:
Same (exact match)	71%
Similar (differ by no more than 1.0)	29%
Different (differ by > 1.0)	0%

Table 4-20. Using the X^2 Test of Independence: Do the three main species-categories differ significantly in their distributions of trunk architecture types?

(Contingency Table:)

Types of Trunk Architecture:		Species Categories: A to B:	AD to BD:	DB to D:	Totals:
Straight:	Observed:	38	10	0	48
	Expected:	26.19	16.04	5.77	48
Twisted:	Observed:	87	39	6	132
	Expected:	72.03	44.11	15.85	132
Gnarled:	Observed:	84	79	40	203
	Expected:	110.8	67.84	24.38	203
	Column Totals:	209	128	46	383

Null Hypothesis: The three main species-categories possess equivalent distributions of straight, twisted, and gnarled trunk architectures.

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 41.5$

df = 4 $\therefore$ where $\alpha = .05$, the critical X^2 value = 9.49

Since 41.5 » 9.49 $\therefore$ strongly reject the Null Hypothesis

Conclusion: The species-categories differ significantly in their trunk architectures (gnarled trunk-form tends to occur most frequently in the DB-D group, and least frequently in the A-B group).

Table 4-21. Using an ANOVA to detect differences in the mean of trunk circumferences at breast height (C.B.H.) of trees belonging to the three trunk architecture groups.

SUMMARY:

Architecture:	*Count*	*Sum*	*Average*	*Variance*
Straight	48	3739	77.90	1602.98
Twisted	132	11850	89.77	1754.71
Gnarled	203	26228	129.20	2337.99

ANOVA: Single Factor

Null Hypothesis: The three categories have the same mean C.B.H.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between categories	178072.83	2	89036.41	43.5172	9.607E-18	3.0195
Within categories	777481.88	380	2046.01			
Total	955554.71	382				

Decision: Reject the Null Hypothesis

Conclusion: The mean C.B.H.'s within the three types of trunk architectures are significantly different (trees with gnarled architecture tend to also have larger circumferences).

Abundance of mite-galls:

Genetically-determined susceptibility to mite-gall infestation provides an opportunity to recognize specific genotypes, and thus specific clones. The spatial distribution of the five categories of gall abundance are displayed in Fig. 4-37. Here, tight clusters of heavily infested individuals appear among the large numbers of lightly affected trees. The groups of heavily impacted trees may share susceptibility due to clonal relatedness.

To better understand how mite-gall susceptibility might be related to other features of the population, gall abundances in the sexes and the species categories were investigated. It was found that the sexes do not differ in their occurrence of mite-galls (Table 4-22), but that the species do (Table 4-23). The intersectional hybrids were found to have a disproportionately higher degree of infestation than that of the pure species and intrasectional hybrid categories. These trends are elaborated upon by Kalischuk et al. (1996).

Since mite-galls accumulate over periods of years, smaller trees would be expected to have fewer galls than larger, presumably older ones. Fig. 4-38 presents the relationship between gall abundance and trunk circumference. Trees with circumferences under 50 cm tended to have few galls, but heavily galled individuals appear in almost every other circumference category. This suggests that even young trees susceptible to mites can host large numbers of galls, especially if the surrounding trees carry heavy infestations.

The population's already non-random spatial arrangement of trunks was discovered to be further clumped in the distribution of sex and species-related characteristics. Patterns in phenology of flowering, leaf flushing, leaf senescence, and leaf drop were found to be species related, with some

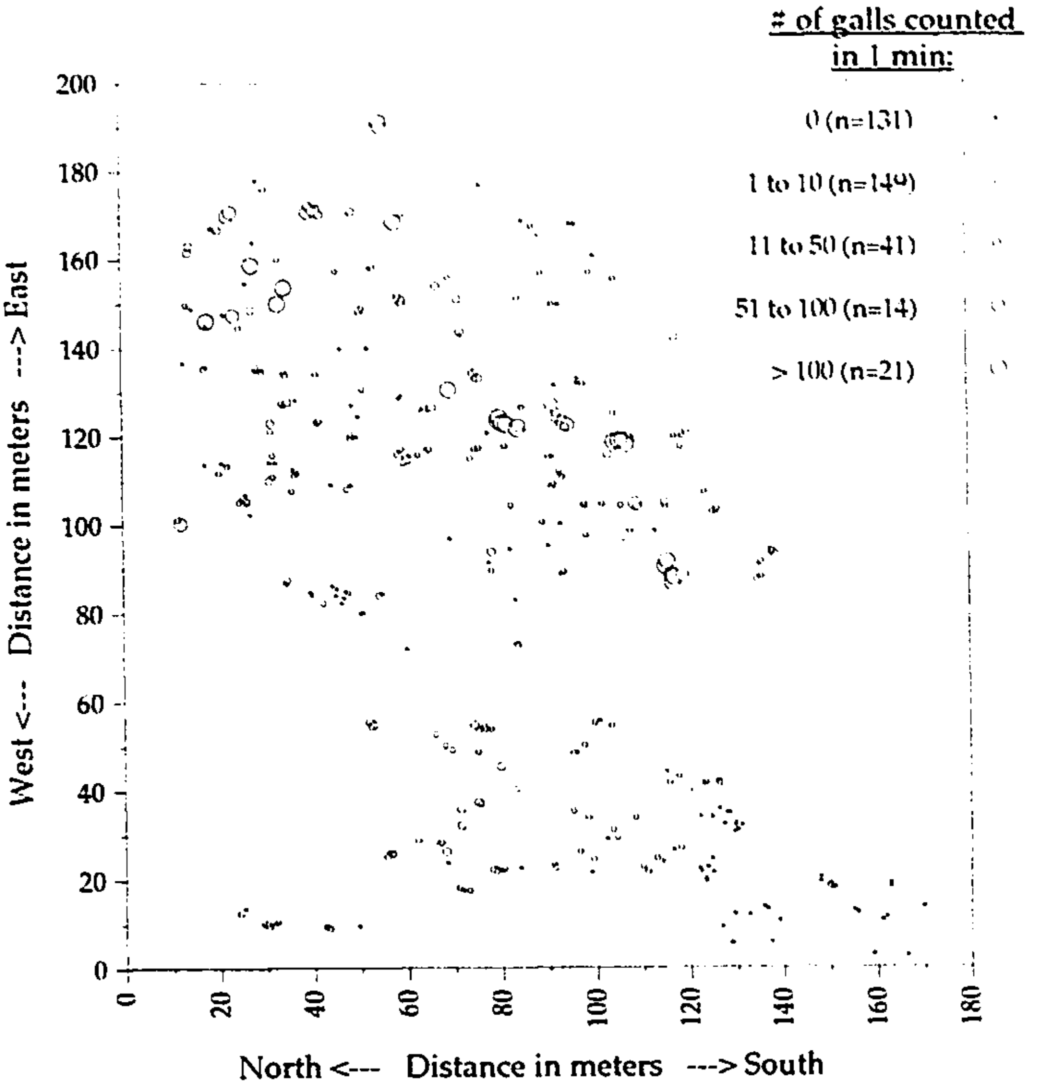


Figure 4-37. The spatial distribution of trunks according to the five gall abundance categories. Gall abundance was classified by the number of galls surveyed during one minute of observation.

Table 4-22. Using the F-Test to determine whether the variance of gall abundance in males is significantly different from that in females, in order to choose the proper t-Test for testing whether the means of the two samples are significantly different.

F-Test: Two-Sample for Variances
Null Hypothesis: The two samples have the same variance.

	Males	*Females*
Mean	18.2793	12.5202
Variance	1467.4940	851.1443
Observations	111	198
Degrees of Freedom	110	197
F	1.7241	
P (F<=f) one-tail	.0004633	
F Critical one-tail	1.31198	

Decision: Do not reject the Null Hypothesis
Conclusion: The variances are not significantly different, therefore use the following t-Test:

t-Test: Two-Sample Assuming Equal Variances
Null Hypothesis: The two samples have the same mean.
(the mean abundances of galls are not significantly different in males versus females)

Degrees of freedom	307
t Stat	1.4835
P (T<=t) one-tail	.06949
t Critical one-tail	1.6498
P (T<=t) two-tail	.13898
t Critical two-tail	1.9677

Decision: Do not reject the Null Hypothesis
Conclusion: The sample means do not differ significantly -mean gall abundance does not differ significantly between the sexes

Table 4-23. Using an ANOVA to detect differences in mean gall abundances among the three species categories; A-B, AD-BD, and DB-D.

SUMMARY:

Categories:	*Count*	*Sum*	*Average*	*Variance*
A to B	195	661	3.39	70.21
AD to BD	118	4311	36.53	2289.82
DB to D	43	99	2.30	9.83

ANOVA: Single Factor

Null Hypothesis: The three categories have the same mean gall abundances.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between categories	87732.93	2	43866.46	54.921	1.71E-21	3.0213
Within categories	281942.81	353	798.70			
Total	369675.74	355				

Decision: Reject the Null Hypothesis

Conclusion: The mean gall abundances of the three species-categories differ significantly (the AD-BD category has a disproportionately higher average abundance of galls).

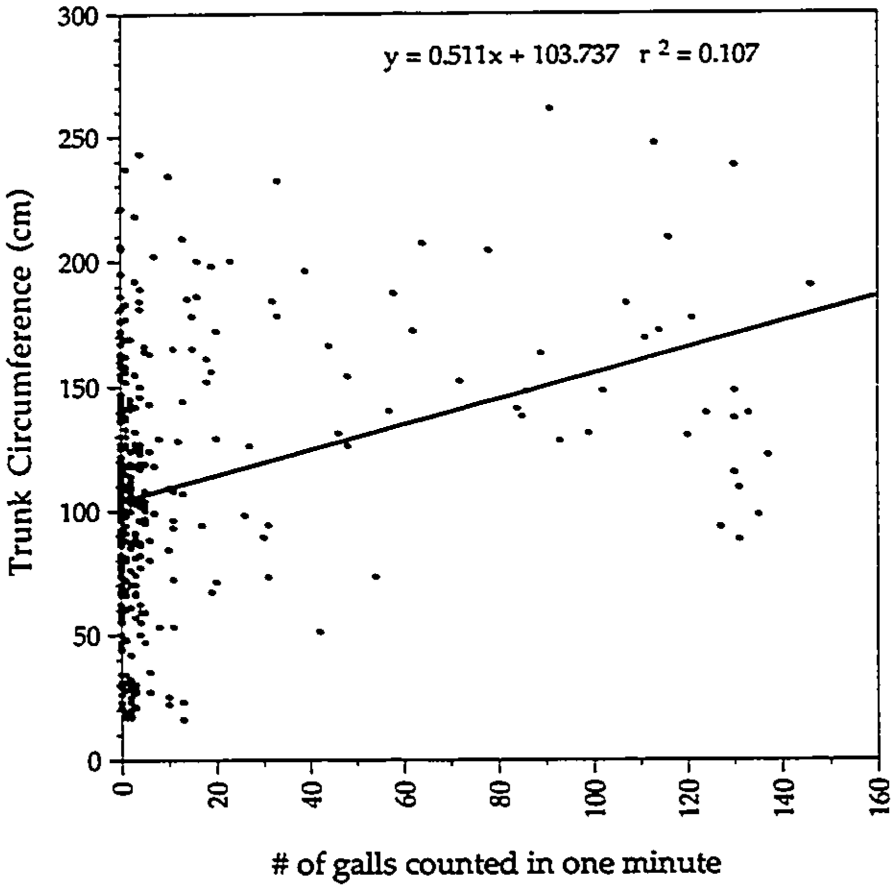


Figure 4-38. The relationship between gall abundance and trunk circumference at breast height (N=356).

potential for individual variation. In some cases, instances of trunk connectivity and shared susceptibility to mite-gall infestation contributed to defining trunk-clusters. By consolidating the clusters discovered in the distributions of the characteristics, a map of potential clones results.

4.2 Half-Sibling Characteristics:

In the minute chance that two or more siblings established next to one another, those individuals would represent the maximum potential for similarity among non-clonally related individuals. To investigate the chance of mistaking such siblings for clones, it was thought prudent to direct a comparison of the potential for sibling versus clonal variability. Leaf dimensions were the only characteristics available for such comparison.

Blade width and petiole length provided an informative index of species-type in earlier evaluations of the population, so these measurements were plotted with those from the field population for each of the 18 sibling groups (Fig. 4-39). The species-type of the maternal source of each sibling group is identified in parentheses. Sibling groups of section *Tacamahaca* show the tightest clustering, while increasing scatter appears for sibling groups of the intersectional hybrids and section *Aigeiros*. These trends might be due to differences in the hybridization tendencies of the different species. Strangely, the petiole measurements from the seedlings were smaller than those from the trees in the mature population. If the juvenile nature of the seedlings is responsible for this trend, the variability of other leaf measurements might also be influenced by immaturity. This complicates the comparison of variability between mature and immature individuals. The trends in half-sibling similarity will be tabled until the leaf measurements of the hypothesized clone groupings are forwarded for comparison and discussion.

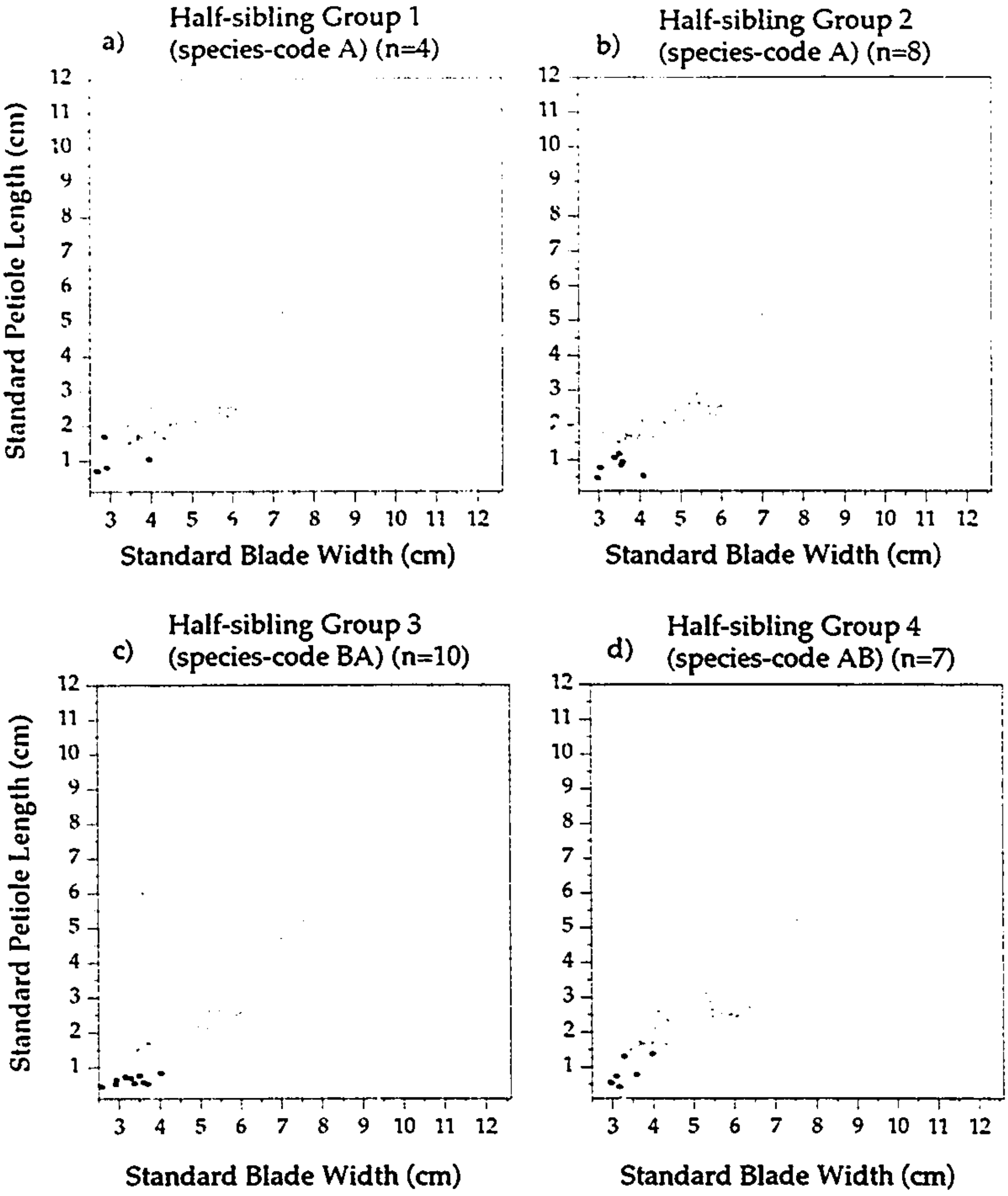
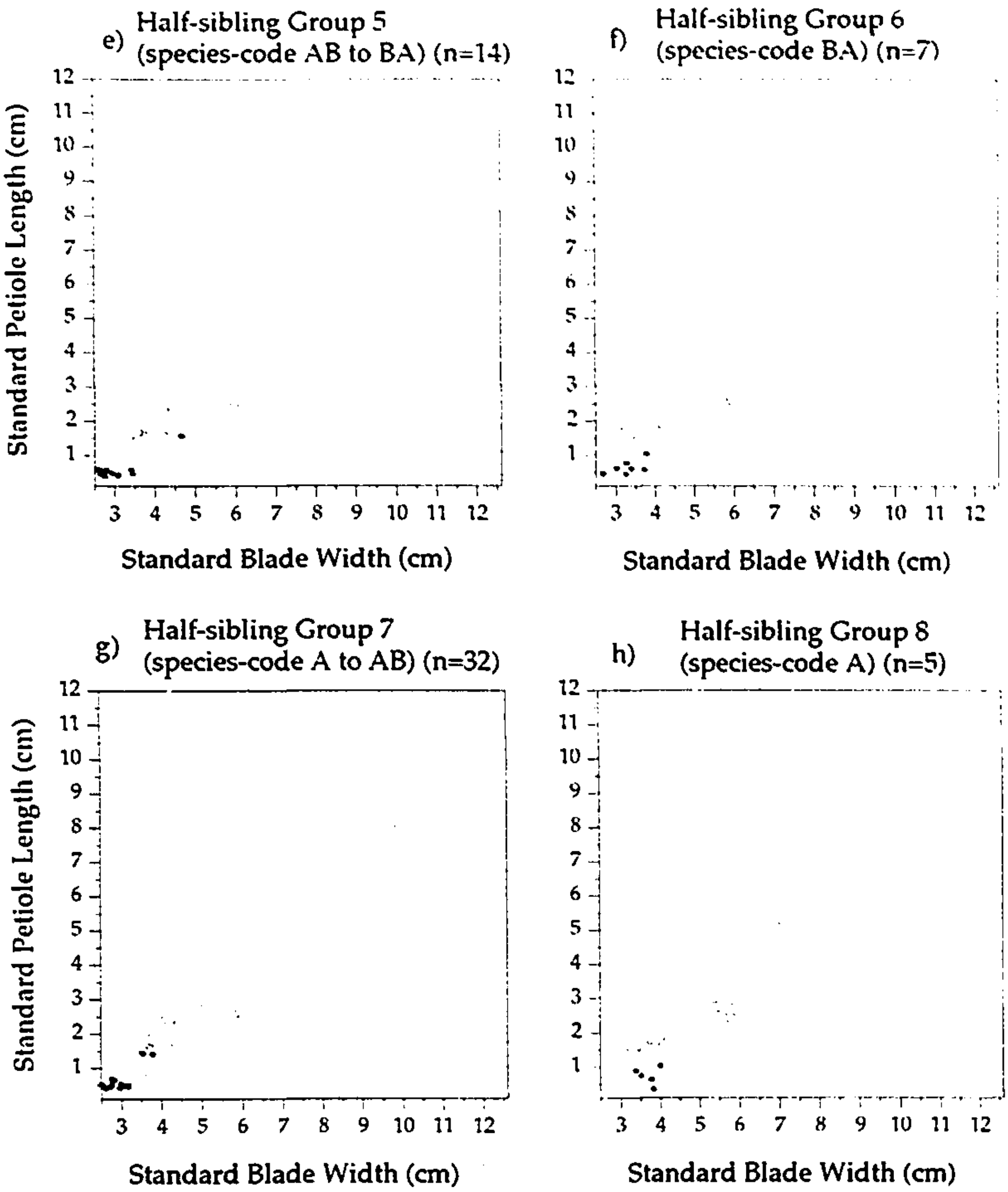
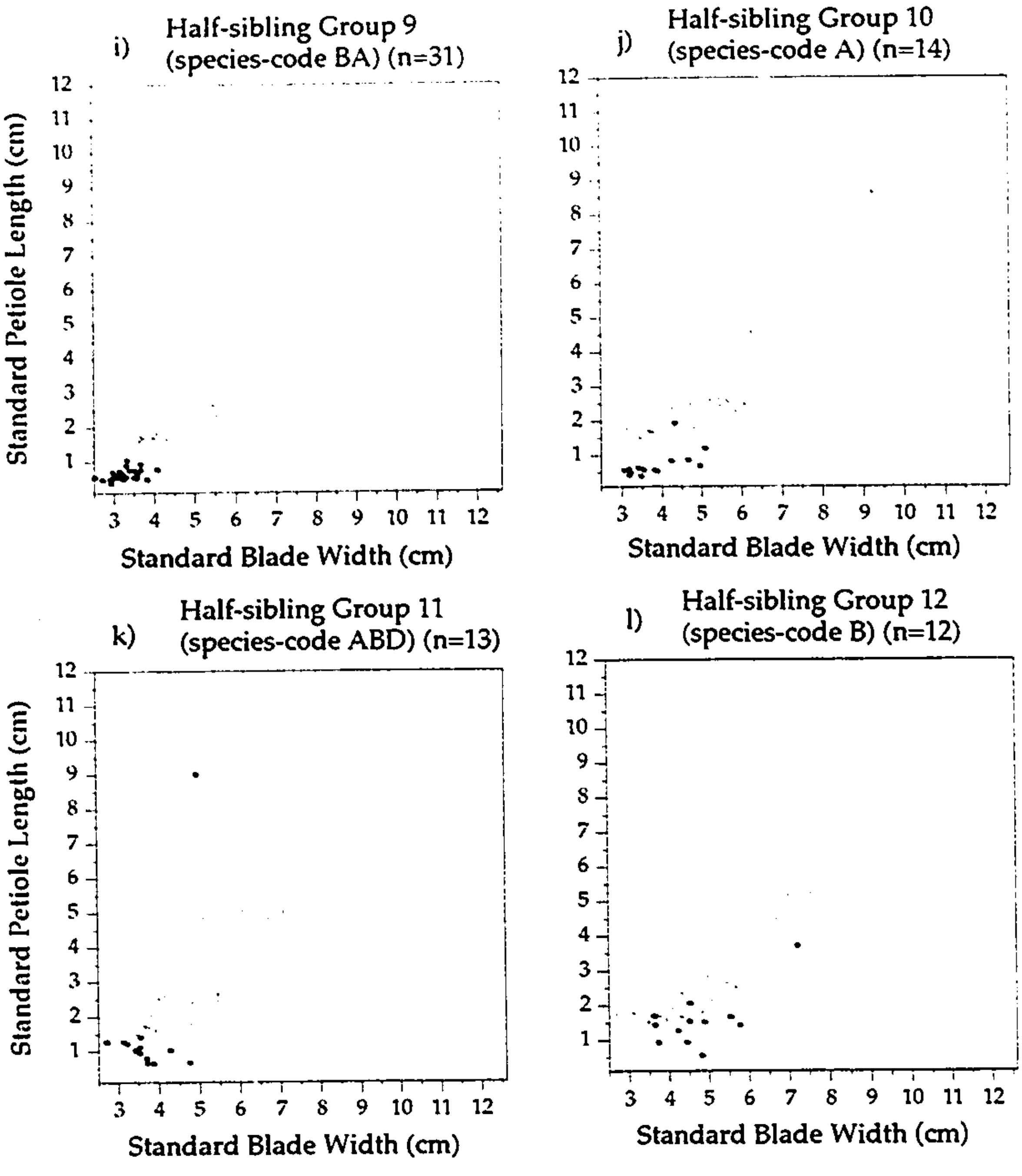


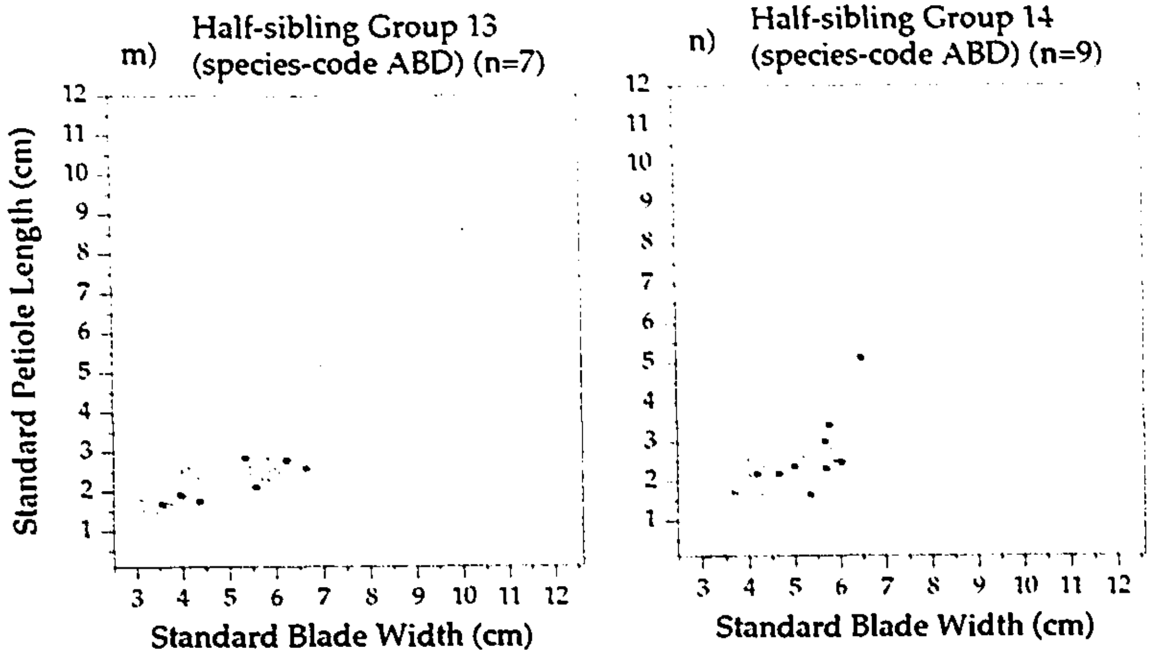
Figure 4-39. Summary of half-sibling leaf measurement similarities (black) as compared with measurements from all trees on the study site (N=391).



Continued - Figure 4-39. Summary of half-sibling leaf measurement similarities (black) as compared with measurements from all trees on the study site (N=391).

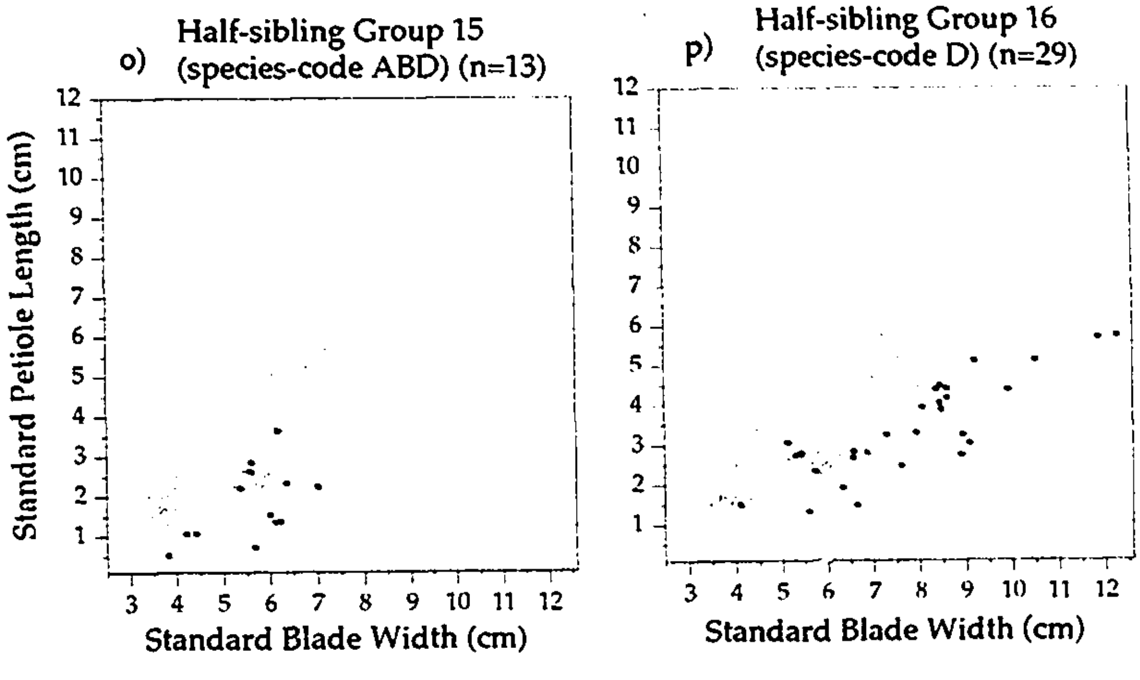


Continued - Figure 4-39. Summary of half-sibling leaf measurement similarities (black) as compared with measurements from all trees on the study site (N=391).



m) Half-sibling Group 13 (species-code ABD) (n=7)

n) Half-sibling Group 14 (species-code ABD) (n=9)

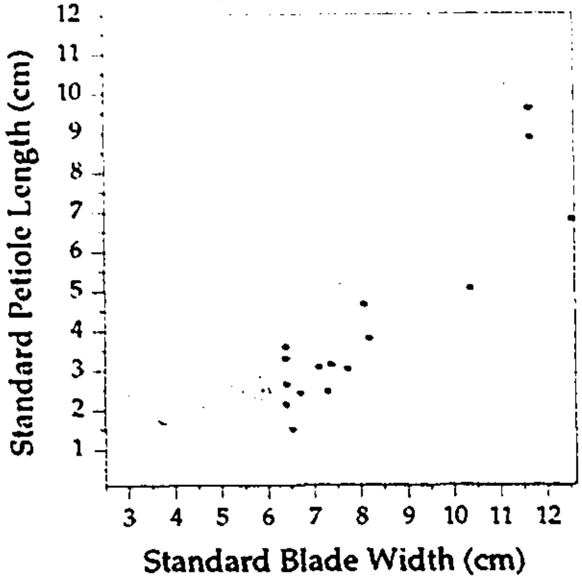


o) Half-sibling Group 15 (species-code ABD) (n=13)

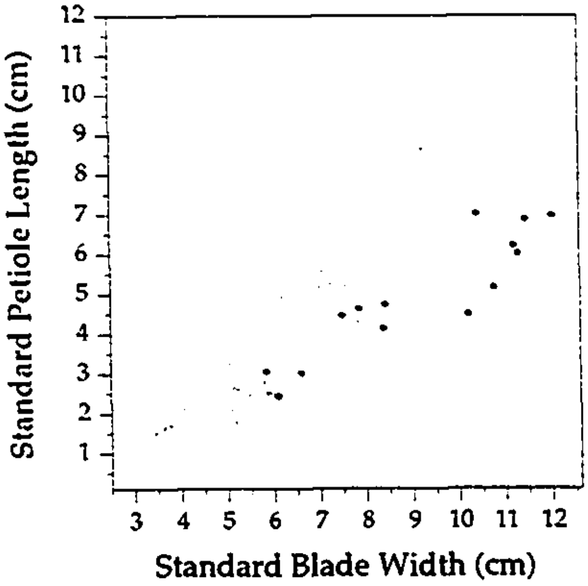
p) Half-sibling Group 16 (species-code D) (n=29)

Continued - Figure 4-39. Summary of half-sibling leaf measurement similarities (black) as compared with measurements from all trees on the study site (N=391).

q) Half-sibling Group 17
(species-code D) (n=18)



r) Half-sibling Group 18
(species-code D) (n=14)



Continued - Figure 4-39. Summary of half-sibling leaf measurement similarities (black) as compared with measurements from all trees on the study site (N=391).

4.3 Identifying Clones:

4.3.1 Constructing groups based on character similarity:

Being discrete and heritable, the character of sex was used to guide the first division of the population. The population of 116 males, 204 females, and 71 unsexed trees was divided to produce two groups; one with 187 trees (116 males and 71 unknowns) and the other with 275 (204 and 71 unknowns). It should be noted that the trees of unknown sex were duplicated in both groups to allow them to be considered in either group.

Species composition was the next most compelling characteristic, so the two sex-defined groups were divided according to leaf shape categories. Overlap between adjacent groups was introduced again so that individuals of intermediate nature could be considered in either category. The category criteria and numbers of trunks for each of the resulting groups are presented in Table 4-24. The spatial distributions of the trunks belonging to each of the twelve groups are illustrated in Fig. 4-40.

To incorporate the phenology characters, the matrix of codes representing the timing of flowering, leaf flush, leaf senescence, and leaf drop was used to subdivide each of the twelve groups. The timing of flowering was given the most significance, except where there was missing information, usually due to immaturity. Divisions were made by individually examining each group for substantial differences in coding. As long as the difference between codes on any given day did not exceed a value of 1, those individuals were left undivided. Where an individual's codes showed a suspicious jump in values, especially where the previous value was a 0, a subjective judgement was made as to whether missing values were responsible, and the appropriate adjustments were made.

Table 4-24. Summary of groups generated by division according to sex and then leaf-shape category. The original dataset contained 391 trunks. Note that overlapped groupings have resulted in a total of 193 redundant entries to this point. Certain species categories did not have representatives of a particular sex or had a particularly small memberships so the categories were defined irregularly.

Group ID:	# of Trunks:	Sex:	Leaf shape codes:
A	16	F + ?'s	1.0 to 1.5
B	61	F + ?'s	1.5 to 2.5
C	94	F + ?'s	2.5 to 3.5
D	59	F + ?'s	3.5 to 4.0
E	92	F + ?'s	5.0 to 5.5
F	29	F + ?'s	7.0 to 8.0
G	15	M + ?'s	1.0 to 1.5
H	47	M + ?'s	1.5 to 2.5
I	53	M + ?'s	2.5 to 3.5
J	71	M + ?'s	5.0 to 5.5
K	23	M + ?'s	5.5 to 6.5
L	24	M + ?'s	6.5 to 8.0

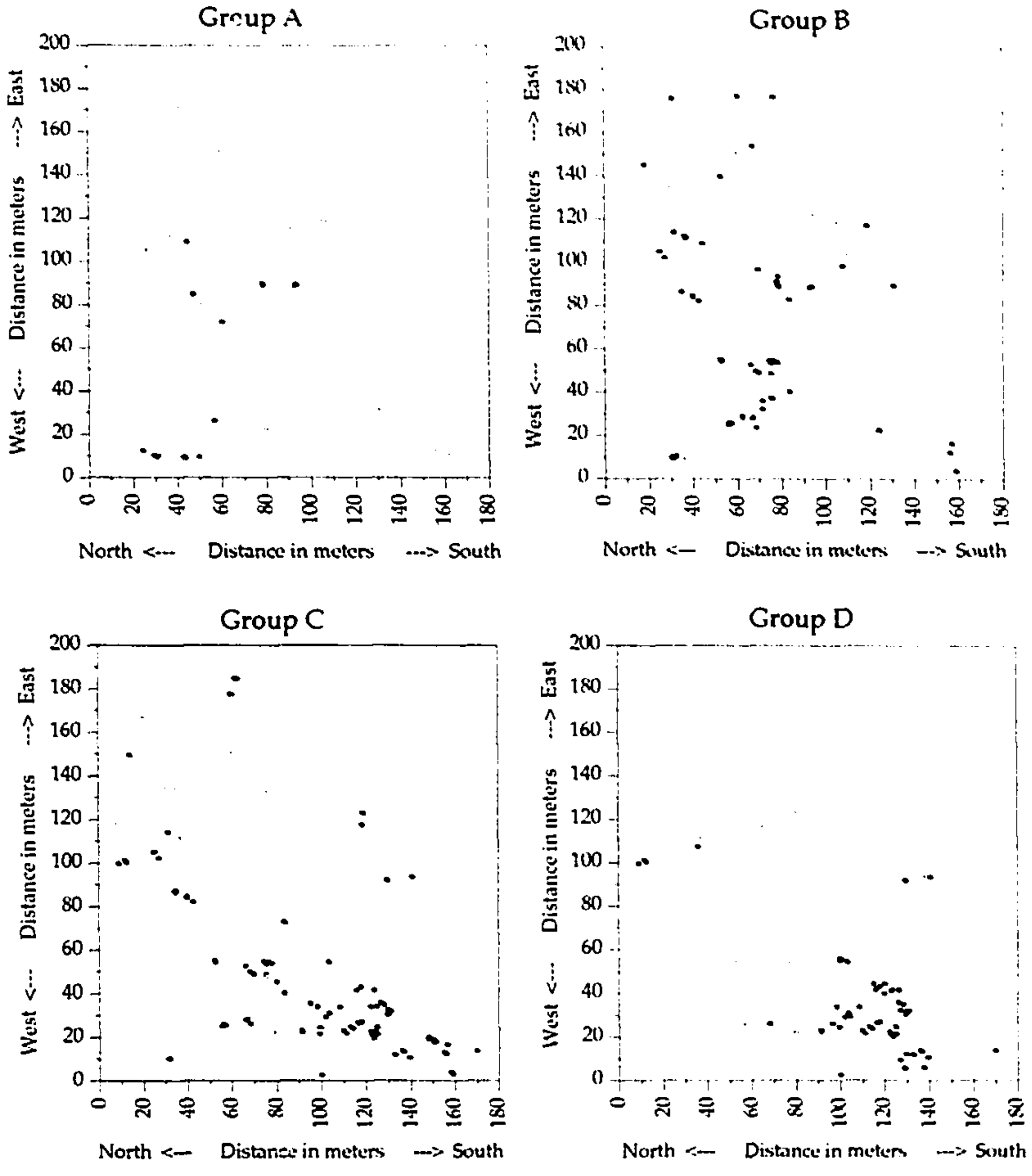
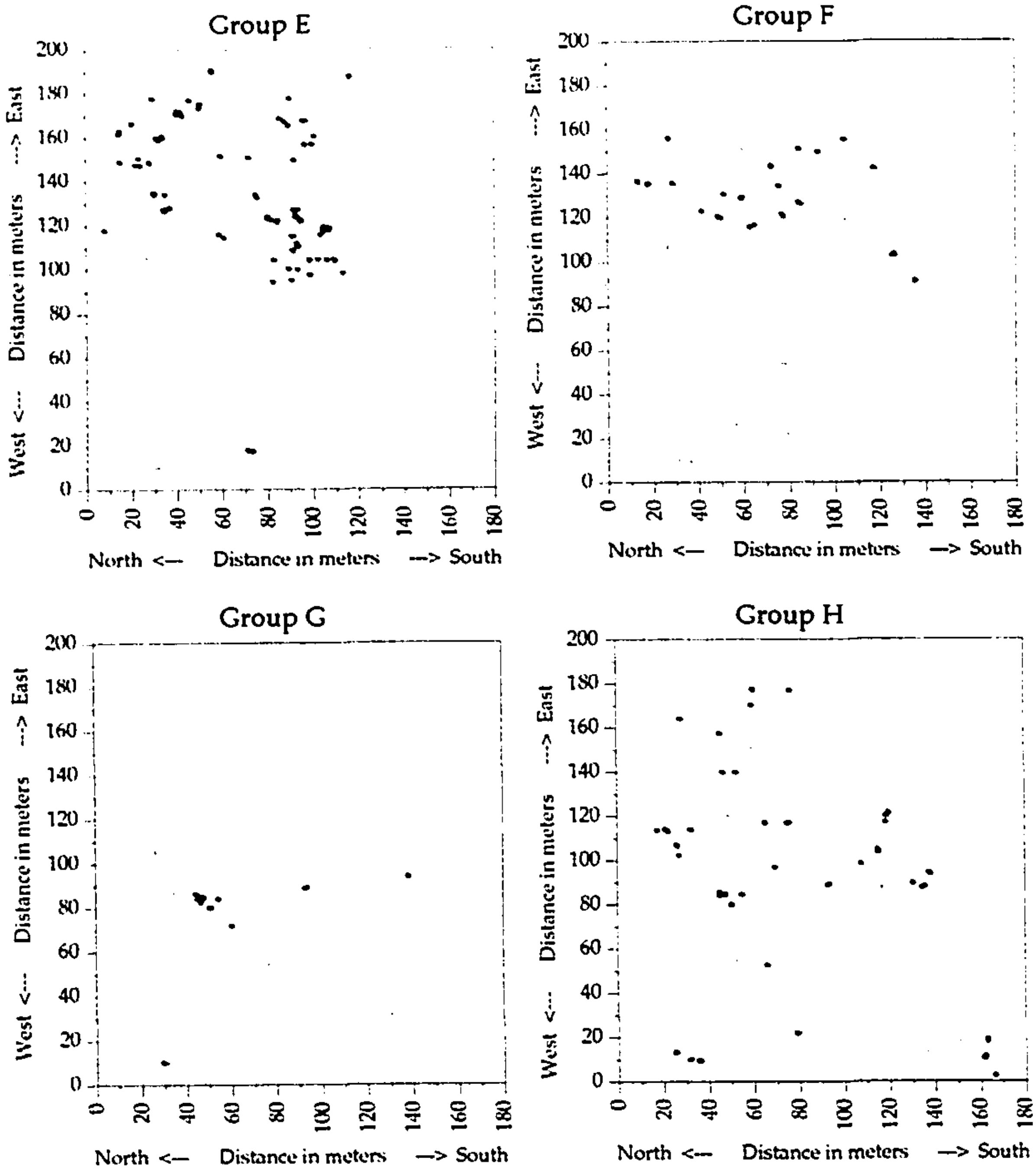
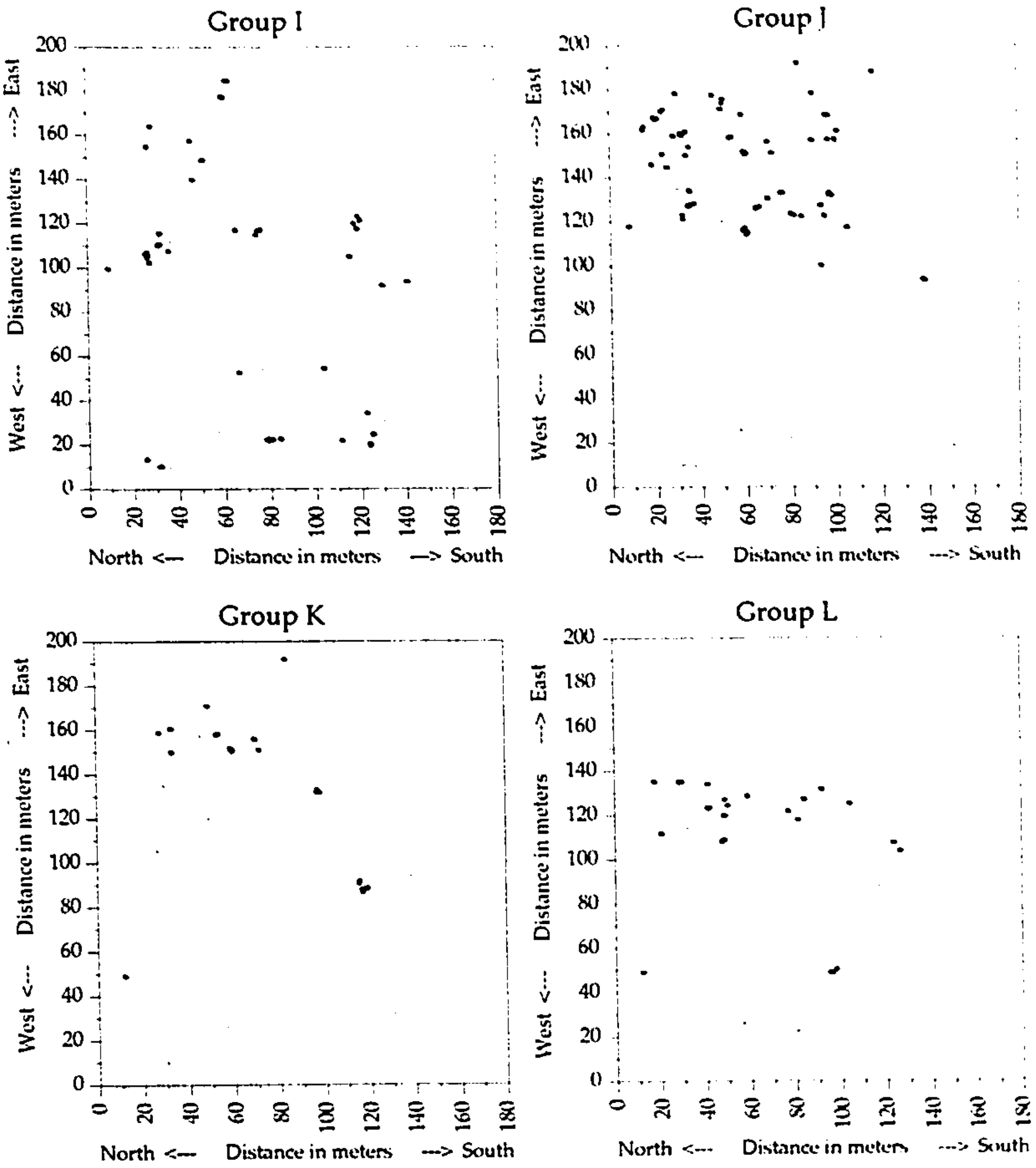


Figure 4-40. The spatial distribution of trunks belonging to Groups A, B, C, and D (black) in relation to the remainder of the population (grey).



Continued - Figure 4-40. The spatial distribution of trunks belonging to Groups E, F, G, and H (black) in relation to the rest of the population (grey).



Continued - Figure 4-40. The spatial distribution of trunks belonging to Groups I, J, K, and L (black) in relation to the rest of the population (grey).

After these divisions, the redundant appearances of trees in more than one clone group were compared. Only the version most closely matching the group to which it had been assigned was retained. In this way, preference was given to any copy assigned to a group rather than occurring singly.

Depending on the spatial distance separating a member from the rest of its group, a final decision was made whether to include it. As a result, the population of 391 was divided into 67 groups of trunks and 48 single trunks. Each of the 67 groups was considered a putative clone and was arbitrarily assigned a reference number. The trees in each group and their associated phenology codes are listed in Table 4-25. Fig. 4-41 illustrates the spatial placement of single trunks and groups, indexed by their reference codes.

Mite-gall abundance, trunk-connectivity, and leaf measurements were used to verify the hypothesized groupings. Gall abundance is cataloged for each tree of each group in Table 4-25. Overall, susceptibility to mite-gall infestation is consistent within the groups. The putative clones 20, 27, 29, 31, 64, and 65 typify these findings, having extremely high numbers of galls recorded for all of their members. Conversely, the majority of the other groups have consistently small gall-counts for their trees. Tree number 138 from clone 27, 315 from clone 36, and 266 from clone 52 had gall-counts which were inconsistent within their groups. Although not conclusive, these differences suggest that these trees might not belong to these clone groups.

The trends in the close spacing of trunks summarized earlier in Tables 4-17, Table 4-18, and Table 4-19, reinforce the groupings so far hypothesized. In every case, the closely spaced trees occurred within the same hypothesized clone grouping. These instances are indicated in Table 4-25 by the boxing together of identification numbers.

Table 4-25. Hypothesized clone groupings based on sex, leaf shape, and phenology similarities. Boxed ID#'s indicate trunks spaced less than 5 cm apart. The column headings are; ID#'s (tree tag number), CBH (circumference at breast height in cm), Sex (M=male, F=female, ?=unknown), Spec (species as interpreted from leaf shape codes), Flowering (coded), Leaf Flush (coded), Senescence (coded), Leaf Drop (coded), Branch Sac. (branch sacrifice; coded), and Gall count (number of galls counted in one minute). Note that blanks replace phenology codes impacted by immaturity or poor health.

Clone	ID#	CBH	Sex	Spec	Flowering									Leaf Flush						Senescence						Leaf Drop					Sac.	count
1	2	147	M	2.5	0.0	1.0	1.0	1.5	2.0	3.0	4.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	2	5	7	9	9	0	0	0	0	4	1	0
	3	176	M	2.5	0.0	1.0	1.0	1.5	2.0	3.0	4.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	2	5	7	8	9	0	0	0	3	4		0
	4	221	M	2.5	0.0	1.0	1.0	1.5	2.0	3.0	4.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	2	5	7	8	9	0	0	0	3	4		0
	5	163	M	2.5	0.0	1.0	1.0	1.5	2.0	3.0	4.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00													X
	6	195	M	2.5																												0
	7	205	M	2.5	0.0	1.0	1.0	1.5	2.0	3.0	4.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	3	5	7	8	9	0	0	0	3	4	1	0
2	8	117	F	2.5	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	2	2	5	7	8	9	0	0	2	4	5		X
	9	118	F	3	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	2	2	5	7	8	9	0	0	2	4	5		0
	10	126	F	2.5																												X
	11	162	F	2.5	0.0	0.0	0.0	0.0	0.0	1.0	2.0	2.5	3.5	0.00	0.00	0.25	1.00	2.00	2.00	2	2	3	6	8	9	0	0	1	3	5		0
	12	122	F	3	0.0	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.5	0.00	0.00	0.25	1.00	2.00	2.00	2	2	4	6	8	9	0	0	1	3	5		0
	13	117	F	3	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	3.5	0.00	0.00	0.25	1.00	2.00	2.00	1	1	3	6	8	9	0	0	0	3	4		0
	14	97	F	3	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	3.5	0.00	0.25	0.25	1.00	2.00	2.00	1	1	3	6	8	9	0	0	0	3	4		0
	15	79	F	3	0.0	0.0	0.0	0.0	0.0	0.0	1.0	3.0	3.5	0.00	0.25	0.25	1.00	2.00	2.00	1	1	3	6	8	9	0	0	0	3	4		1
	16	77	F	3	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	3.5	0.00	0.25	0.25	1.00	2.00	2.00	1	1	3	6	8	9	0	0	0	3	4		0
	17	112	F	3	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	3.5	0.00	0.25	0.25	1.00	2.00	2.00	1	1	3	6	8	9	0	0	1	3	5		0
	18	111	F	3	0.0	0.0	0.0	0.0	0.5	1.0	2.0	3.0	3.5	0.00	0.25	0.25	1.00	2.00	2.00	1	1	3	6	8	9	0	0	1	3	5		0
3	19	115	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	1	3	6	8	9	0	0	0	1	5		0
	20	118	F	4	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	1	4	6	8	9	0	0	0	1	5		0
	21	98	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	1	3	6	8	9	0	0	0	1	5		0
	22	162	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	1	3	6	8	9	0	0	0	1	5		0
	23	110	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	1	3	6	8	9	0	0	0	1	5		0
	24	100	F	4	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	1	3	6	8	9	0	0	0	1	5		0
	25	145	F	4	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	1	4	6	8	9	0	0	0	1	5		0
	26	169	F	4	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	1	3	6	8	9	0	0	0	1	5		0
	27	138	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	0	1	6		0
	28	155	F	2.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	0	1	6		0
	29	118	?	3.5										0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	0	3	6		0
	381	142	?	3										0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	0	3	6		0
	30	156	F	3.5	1.5	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	0	3	6		0
	31	127	F	3.5	0.5	1.0	2.0	2.5	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	0	3	6		0
	32	28	?	3.5										0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	3	3	6		0
	33	76	?	3										0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	1	3	6		0
	34	98	F	3	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	1	3	6		0
	35	94	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	0	1	5		0
	36	141	F	4	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	0	1	5		0
	37	65	F	4	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	0	1	5		0
	382	109	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	0	1	5		0
	38	117	F	3	1.5	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	0	1	5		0
	383	119	F	4	1.5	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	0	1	5		0
	39	91	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	0	1	5		0

Continued - Table 4-25. Hypothesized clone groupings based on sex, leaf shape, and phenology similarities.

	ID#	CBH	Sex	Spec	Flowering									Leaf Flush						Senescence						Leaf Drop					BSac.	Galls
	40	60	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	1	3	6		0
	384	19	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	1	3	6		0
	385	17	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	1	3	6		0
	41	137	F	3.5	0.5	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	2	3	6		1
	42	72	F	3.5	1.0	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	2	3	6		0
	43	183	F	3.5	0.5	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	2	2	6		0
	44	88	F	3.5	1.0	1.5	2.5	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	2	3	6		1
	45	158	F	3.5	1.0	1.5	2.5	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	2	2	5		2
	46	141	F	3	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	3	6		0
	47	133	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	3	6		2
	48	138	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	1	5		0
	49	130	F	3.5	1.0	2.0	2.5	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	1	5		2
	50	107	F	4	1.0	1.5	2.5	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	1	5		1
	52	34	?	3.5										0.00	1.00	2.00	2.00	2.00	2.00	0	0	2	6	9	9	0	0	2	5	7		1
	53	177	F	3.5	1.0	1.5	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	5	7	9	0	0	0	0	4		3
	54	141	F	3.5	1.0	1.5	2.5	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	5	7	9	0	0	0	0	4		2
	55	112	F	4	0.5	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	4	6		2
	56	126	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	3	6		4
	57	144	F	3	0.0	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	3	6		10
	91	61	F	4	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	0	3	6		2
	92	76	F	4	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	0	3	5		2
	93	124	F	4	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	9	9	0	0	0	3	6		0
	94	81	F	3.5	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	9	9	0	0	0	3	6		2
	95	100	F	4	1.0	2.0	3.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	9	9	0	0	0	3	6		3
	96	87	F	4	1.0	1.5	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	9	9	0	0	0	3	6		5
	97	100	F	3.5	1.0	2.0	2.5	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	9	9	0	0	0	3	6		1
	98	80	F	3.5	1.0	2.0	2.5	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	9	9	0	0	0	3	6		3
	99	110	F	4	0.0	1.0	2.0	2.5	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	2	7	9	9	0	0	0	3	6		0
	380	?	F	3.5	0.5	1.0	2.0	3.0	3.5	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00													X
4	58	101	M	3	0.0	1.0	1.5	2.0	2.5	3.0	3.0	4.5	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	0	0	3	7	9	0	0	0	0	4		0
	59	119	M	3	0.0	1.0	1.5	2.0	2.5	3.0	3.0	4.5	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	0	0	3	7	9	0	0	0	0	4		0
	60	102	M	2.5	0.0	1.0	1.5	2.0	2.5	3.0	3.0	4.5	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	0	0	3	7	9	0	0	0	0	4		4
	386	107	M	3	0.0	1.0	1.5	2.0	2.5	3.0	3.0	4.5	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	0	0	3	7	9	0	0	0	0	4		1
	387	121	M	3	0.0	1.0	1.5	2.0	2.5	3.0	3.0	4.5	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	0	0	3	7	9	0	0	0	0	4		1
	388	91	M	3	0.0	1.0	1.5	2.0	2.5	3.0	3.0	4.5	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	0	0	3	7	9	0	0	0	0	4		0
5	61	155	F	5	0.0	0.0	0.0	0.0	0.5	1.0	2.0	3.0	3.0	0.00	0.25	0.25	1.00	2.00	2.00	0	0	0	2	6	9	0	0	4	5	6		0
	62	146	F	5	0.0	0.0	0.0	0.0	0.5	1.0	2.0	3.0	3.5	0.00	0.25	0.25	1.00	2.00	2.00	0	0	0	2	6	9	0	0	4	5	6		2
	389	123	F	5	0.0	0.0	0.0	0.0	0.5	1.0	2.0	3.0	3.5	0.00	0.25	0.25	1.00	2.00	2.00	0	0	0	2	6	9	0	0	4	5	6		3
6	63	96	F	2	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	1	3	7	8	9	0	0	2	3	5		0
	64	114	F	3.5	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	1	3	7	8	9	0	0	2	3	5	1	42
	65	86	F	2.5	0.0	0.0	0.0	0.0	0.5	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	1	3	7	8	9	0	0	2	3	5		6
	66	91	F	2.5	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	1	3	7	8	9	0	0	2	3	5		7
	67	109	F	2	0.0	0.0	0.0	0.5	1.5	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	1	3	7	8	9	0	0	2	3	5	1	4
	68	100	F	2	0.0	0.0	0.0	1.0	2.0	3.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	1	3	7	8	9	0	0	2	3	5		16
	69	60	F	2	0.0	0.0	0.5	1.0	2.0	2.5	3.0	3.5	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	1	3	7	8	9	0	0	2	4	6		33
	70	100	F	2	0.0	0.0	0.0	0.5	1.5	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	1	3	7	8	9	0	0	2	3	6		48
	71	103	F	2	0.0	0.0	0.0	0.5	1.5	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	1	3	7	8	9	0	0	2	3	5		1
	107	108	F	2.5	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	2	4	7	8	9	0	0	3	4	6		10
	108	114	F	3	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	2	4	7	8	9	0	0	3	4	6		31
	109	82	F	2.5	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	2	3	7	8	9	0	0	3	4	6		6
	110	73	F	2.5	0.0	0.0	0.0	0.0	0.5	1.5	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	5	6	9	9	9	9	4	4	5	7	6		5
	111	87	F	2	0.0	0.0	0.0	0.0	1.0	1.5	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	2	3	7	8	9	0	0	3	4	6		6
	112	60	F	2.5	0.0	0.0	0.0	0.0	0.5	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	2	3	7	8	9	0	0	3	4	6		10
	113	82	F	2.5	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	2	3	7	8	9	0	0	3	4	6		13
	114	44	F	2.5	0.0	0.0	0.0	0.0	0.5	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	2	3	7	8	9	0	0	3	4	6		2
	115	100	F	2.5	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	2	3	7	8	9	1	0	3	4	6		5

Continued - Table 4-25. Hypothesized clone groupings based on sex, leaf shape, and phenology similarities.

	ID#	CBH	Sex	Spec	Flowering									Leaf Flush						Senescence						Leaf Drop					RSac.	Galls
	116	79	F	2.5	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	1	2	3	7	8	9	0	0	3	4	6		10
	117	70	?	2.5										0.25	0.25	1.00	2.00	2.00	2.00	2	2	3	7	8	9	0	0	5	5	7		4
7	72	117	F	2.5	0.0	0.0	0.0	0.0	0.0	1.0	2.0	2.5	3.0	0.00	0.00	0.25	0.25	1.00	1.00	0	1	2	7	8	9	0	0	3	3	5		5
	73	172	F	2.5	0.0	0.0	0.0	0.0	0.0	1.0	2.0	2.5	3.0	0.00	0.00	0.25	0.25	1.00	1.00	0	1	2	7	8	9	0	0	3	3	5		0
	74	170	F	1	0.0	0.0	0.0	0.0	0.0	1.0	2.0	2.5	3.0	0.00	0.00	0.25	0.25	1.00	1.00	0	1	2	7	8	9	0	0	3	3	5		3
	75	167	F	2.5	0.0	0.0	0.0	0.0	0.0	1.0	2.0	2.5	3.0	0.00	0.00	0.25	0.25	1.00	1.00	0	1	2	7	8	9	0	0	3	3	5		2
8	77	160	F	1	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	3.0	0.00	0.25	0.50	1.00	2.00	2.00	0	0	0	1	5	9	0	0	0	0	3	1	3
	78	115	F	1	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	3.0	0.00	0.25	0.50	1.00	2.00	2.00	0	0	0	1	5	9	0	0	0	0	3		0
	79	105	F	1	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	3.0	0.00	0.25	0.50	1.00	2.00	2.00	0	0	0	1	5	9	0	0	0	0	3		3
9	80	85	M	2	0.0	0.0	0.5	1.0	1.5	2.0	3.0	4.0	5.0	0.00	0.25	0.50	1.00	2.00	2.00													X
	81	63	M	2	0.0	0.0	0.5	1.0	1.5	2.0	3.0	4.0	5.0	0.00	0.25	0.50	1.00	2.00	2.00													X
	88	110	M	2.5	0.0	0.0	0.0	1.0	1.5	1.5	3.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	1	3	7	9	9	0	0	0	3	5		0
10	82	112	F	2	0.0	0.0	0.0	0.0	0.5	1.5	2.0	3.0	3.5	0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	9	9	9	0	0	2	4	6		3
	83	55	?	2.5										0.00	0.25	1.00	2.00	2.00	2.00	0	0	0	9	9	9	0	0	0	3	5		0
	84	139	F	1	0.0	0.0	0.0	0.0	0.5	1.5	2.0	3.0	3.5	0.00	0.25	1.00	2.00	2.00	2.00	0	0	0	9	9	9	0	0	2	4	5		0
	85	137	F	1.5	0.0	0.0	0.0	0.0	0.5	1.5	2.0	3.0	3.5	0.00	0.25	1.00	2.00	2.00	2.00	0	0	6	9	9	9	0	0	2	4	6		8
	86	181	F	2	0.0	0.0	0.0	0.0	0.5	1.5	2.0	3.0	3.5	0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	9	9	9	0	0	2	4	6		3
	87	81	?	1										0.00	0.25	1.00	2.00	2.00	2.00	6	7	9	9	9	9	1	3	2	7	6		1
	89	186	F	1	0.0	0.0	0.0	0.0	0.5	1.5	2.0	3.0	3.5	0.25	0.25	1.00	2.00	2.00	2.00	2	5	7	9	9	9	0	1	3	5	6		4
11	118	66	F	2.5	0.0	0.0	0.0	0.5	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	2	3	6	9	9	9	0	0	2	5	7		5
	120	56	F	2	0.0	0.0	0.0	0.5	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	2	3	6	9	9	9	0	0	2	5	7		15
	119	58	F	2.5	0.0	0.0	0.0	0.5	1.0	2.0	3.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	2	3	6	9	9	9	0	0	2	5	7		13
12	104	238	M	8	1.0	2.0	3.0	3.0	4.0	5.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	1	6	9	0	0	0	3	5	3	1
	105	209	M	8	1.0	2.0	2.5	3.0	4.0	5.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	0	6	9	0	0	0	3	5	3	0
	106	238	M	8	1.0	2.0	2.5	3.0	4.0	5.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	0	6	9	0	0	0	3	5	3	2
13	101	31	?	3.5										0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	7	9	9	0	0	0	5	6		1
	102	42	F	4	0.0	1.0	1.5	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	3	7	9	9	0	0	0	5	6		2
	103	32	F	4	0.0	1.0	1.5	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	3	7	9	9	0	0	0	5	6		0
	395	28	F	4	0.0	1.0	1.5	3.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	3	7	9	9	0	0	0	5	6		1
14	100	50	F	3	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.00	0.25	0.25	0.25	1.00	1.00	2	3	6	9	9	9	0	0	2	4	6		8
	390	67	F	3	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.00	0.25	0.25	0.25	1.00	1.00	2	3	6	9	9	9	0	0	2	4	6		2
15	161	110	F	2	0.0	0.0	0.0	0.0	1.0	2.5	3.0	3.5	4.0	0.00	0.25	1.00	2.00	2.00	2.00	7	7	9	9	9	9	1	4	5	5	7		0
	163	23	?	1.5										0.25	0.25	1.00	2.00	2.00	2.00	5	6	9	9	9	9	4	4	5	5	7		0
	164	23	?	1.5										0.25	0.25	1.00	2.00	2.00	2.00	5	6	9	9	9	9	4	4	5	5	7		4
	178	110	F	2	0.0	0.0	0.0	0.0	1.0	2.5	3.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	7	7	9	9	9	9	1	4	5	5	7		13
	179	160	F	2	0.0	0.0	0.0	0.5	1.0	2.5	3.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	7	7	9	9	9	9	1	4	5	5	7		0
	180	114	F	1.5	0.0	0.0	0.0	0.0	1.0	2.5	3.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	7	7	9	9	9	9	1	4	5	5	7		4
	392	67	F	1.5										0.25	0.25	1.00	2.00	2.00	2.00	7	7	9	9	9	9	1	4	5	5	7		X
	181	107	?	2										0.00	0.25	1.00	2.00	2.00	2.00	5	7	9	9	9	9	1	1	3	5	7		0
16	228	116	M	1	0.0	0.0	0.0	0.5	1.0	2.0	3.0	4.5	4.0	0.25	0.25	1.00	2.00	2.00	2.00	1	1	6	7	9	9	0	1	3	4	6		0
	229	139	M	1.5	0.0	0.5	1.0	2.0	2.0	3.0	4.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	2	3	6	7	9	9	0	3	3	5	6		0
	230	104	M	1.5	0.0	0.5	1.0	2.0	2.0	3.0	4.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	3	6	7	9	9	0	1	3	4	6		0
	231	82	M	1	0.0	0.5	1.0	2.0	2.0	3.0	4.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	3	6	7	9	9	0	1	3	4	6		0
	233	81	M	1	0.0	0.5	1.0	1.5	2.0	3.0	4.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	3	6	7	9	9	0	1	3	4	6		0
	234	57	?	1										0.25	0.25	1.00	2.00	2.00	2.00	1	3	6	7	9	9	0	1	3	4	6		0
	235	82	M	1.5	0.0	0.5	1.0	2.0	2.0	3.0	4.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	3	6	7	9	9	0	1	3	4	6		2
	236	121	M	1.5	0.0	0.5	1.0	2.0	2.0	3.0	4.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	3	6	7	9	9	0	1	3	4	6		0
	237	92	M	1	0.0	0.5	1.0	2.0	2.0	3.0	4.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	3	6	7	9	9	0	1	3	4	6		0
	238	102	M	1	0.0	0.5	1.0	2.0	2.0	3.0	4.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	2	5	9	7	9	9	1	4	4	4	6		1
	239	78	M	2	0.0	0.5	1.0	2.0	2.0	3.0	4.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	3	6	7	9	9	0	1	3	4	6		0
17	225	127	F	2.5	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	2	3	6	7	9	9	0	1	3	5	6		0
	226	119	F	2.5	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	2	3	6	7	9	9	0	3	3	5	6		0
	227	97	F	2.5	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.25	0.25	2.00	2.00	2.00	2.00	2	3	6	7	9	9	0	3	3	5	6		1
18	223	125	F	3	0.0	0.0	0.0	0.5	1.0	2.0	3.0	3.5	4.0	0.00	0.25	1.00	2.00	2.00	2.00	2	3	6	7	9	9	0	1	3	4	6	1	0
	224	153	F	3	0.0	0.0	0.0	0.5	1.0	2.0	3.0	3.5	4.0	0.00	0.25	1.00	2.00	2.00	2.00	2	3	6	7	9	9	0	1	3	4	6	1	3
	232	143	F	2.5	0.0	0.0	0.0	0.5	1.0	2.0	3.0	3.5	4.0	0.00	0.25	1.00	2.00	2.00	2.00	2	3	6	7	9	9	0	1	3	4	6	1	0

Continued - Table 4-25. Hypothesized clone groupings based on sex, leaf shape, and phenology similarities.

	ID#	CBH	Sex	Spec	Flowering									Leaf Flush						Senescence						Leaf Drop					BSac.	Calls
19	146	67	F	5	1.0	2.0	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	3	5	7		1
	147	96	F	5	1.5	2.0	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	3	5	7		3
	157	81	F	5	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	3	5	7		0
	159	105	F	5	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	4	5	7		1
	160	91	F	5	1.0	2.0	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	4	5	7		0
	162	89	F	5	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	7	7	8	9	0	1	5	5	7		0
	165	77	F	5	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	3	5	7		6
	166	87	F	5	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	3	5	7		1
	167	20	?	5										0.00	0.25	1.00	2.00	2.00	2.00	0	0	2	7	8	9	0	0	5	5	7		0
	168	86	F	5	1.0	2.0	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	5	5	7		5
	169	50	F	5	1.0	1.0	2.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	7	6	8	9	0	1	5	5	7		3
	170	102	F	5	1.0	2.0	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	4	5	7		3
	171	55	F	5	1.0	2.0	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	4	5	7		1
	172	62	F	5	1.0	1.0	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	5	5	7		2
	173	125	F	5	1.0	2.0	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	1	5	7		0
	174	119	F	5	1.0	1.5	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	1	5	7		1
	175	118	F	5	1.0	1.5	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	1	5	7		0
	176	82	F	5	1.0	1.5	2.5	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	1.00	2.00	2.00	0	0	1	6	8	9	0	0	1	5	7		2
20	132	98	M	6	3.0	4.0	4.0	4.0	4.0	4.0	5.0	5.0	5.0	0.00	0.25	2.00	2.00	2.00	2.00	0	1	2	6	8	9	0	0	3	5	7		85
	152	184	M	6	3.0	4.0	4.0	4.0	4.0	4.0	5.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	2	6	8	9	0	0	3	5	7		135
	153	126	M	6	3.0	4.0	4.0	4.0	4.0	4.0	5.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	2	6	8	9	0	0	4	5	7		130
	154	89	M	6	3.0	4.0	4.0	4.0	4.0	4.0	5.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	2	6	8	9	0	0	3	5	7		130
	155	94	M	6	3.0	4.0	4.0	4.0	4.0	5.0	5.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	2	6	8	9	0	0	4	5	7		130
	156	73	M	6	3.0	4.0	4.0	4.0	4.0	5.0	5.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	2	6	8	9	0	0	4	5	7		130
21	123	160	M	2																												0
	124	206	M	1.5																												4
	128	60	M	2																												3
	129	136	M	2	0.0	0.0	0.0	0.0	0.5	1.5	2.0	3.0	3.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	4	7	8	9	0	0	0	3	6		4
	130	123	?	2																												X
22	126	152	F	8	0.0	0.0	0.5	1.0	2.0	4.0	4.0	4.0	4.0	0.00	0.25	0.25	0.25	0.25	1.00	0	0	0	0	0	7	0	0	0	0	3	2	1
	127	140	F	8	0.0	0.0	0.5	1.0	2.0	4.0	4.0	4.0	4.0	0.00	0.25	0.25	0.25	0.25	1.00	0	0	0	0	0	7	0	0	0	0	3	3	0
23	133	138	F	8	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	0.25	1.00	0	0	0	0	6	9	0	0	0	0	4	2	2
	134	131	F	8	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.00	0.25	0.25	0.25	0.25	1.00	0	0	0	0	6	9	0	0	0	0	4	2	5
	135	126	?	8																												1
24	150	97	M	2.5	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	4	7	8	9	0	0	0	3	6		19
	151	45	M	2	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	4	7	8	9	0	0	0	3	6		1
25	148	150	F	5	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	1	1	6	8	9	0	0	3	5	6		15
	149	102	F	5	0.0	0.0	0.0	0.0	0.5	1.0	2.0	3.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	1	1	6	8	9	0	0	3	5	6		54
26	137	99	?	2.5																												1
	351	105	M	3	0.0	1.0	1.5	2.0	2.0	3.0	4.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	2	7	9	9	0	0	0	4	6		4
	352	117	M	2	0.0	1.0	1.5	2.0	2.0	3.0	4.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	2	7	9	9	0	0	0	4	6		7
	353	145	M	2.5	1.0	1.0	1.5	2.0	2.0	3.0	4.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	2	7	9	9	0	0	0	4	5		18
	354	134	?	3																												X
27	138	125	F	5																												18
	139	110	?	5																												X
	140	88	F	5	0.0	0.0	0.0	0.0	1.0	1.5	3.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	5	7	9	0	0	0	3	5		133
	141	127	F	5																												X
	142	100	F	5	0.0	0.0	0.0	0.0	1.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	5	7	9	0	0	0	3	5		111
	143	108	F	5	0.0	0.0	0.0	0.0	1.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	5	7	9	0	0	0	3	5		93
	145	80	F	5	0.0	0.0	0.0	0.0	0.5	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	5	7	9	0	0	0	3	5		131
	144	96	F	5	0.0	0.0	0.0	0.0	0.5	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	5	7	9	0	0	0	3	5		120
28	338	200	M	5.5	1.0	2.0	2.0	2.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	0.25	1.00	2.00	2.00	1	2	5	7	8	9	0	0	3	5	6		0
	339	94	M	5.5	1.0	2.0	2.0	2.0	2.5	4.0	5.0	5.0	5.0	0.00	0.00	0.25	1.00	2.00	2.00	1	2	5	7	8	9	0	0	3	5	6		0
	340	67	M	5.5	1.0	2.0	2.0	2.0	2.5	4.0	5.0	5.0	5.0	0.00	0.00	0.25	1.00	2.00	2.00	1	2	5	7	8	9	0	0	3	5	7		4

Continued - Table 4-25. Hypothesized clone groupings based on sex, leaf shape, and phenology similarities.

	ID#	CBH	Sex	Spec	Flowering									Leaf Flush						Senescence						Leaf Drop					RNac.	Galls
29	330	117	F	5	1.0	1.5	2.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.00	1.00	2.00	2.00	2.00	0	0	0	1	7	9	0	0	0	4	6	1	17
	331	166	F	5	1.0	1.5	2.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.00	1.00	2.00	2.00	2.00	0	0	0	1	7	9	0	0	0	4	6	1	58
	332	57	?	5										0.00	0.25	1.00	2.00	2.00	2.00	0	0	0	1	7	9	0	0	0	5	6	1	86
	333	59	F	5	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.00	1.00	2.00	2.00	2.00	0	0	0	1	7	9	0	0	0	4	6	1	30
	334	150	F	5	1.0	1.5	2.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.00	1.00	2.00	2.00	2.00	0	0	0	1	7	9	0	0	0	3	6	1	46
	335	59	F	5	0.0	1.0	2.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.00	1.00	2.00	2.00	2.00	0	0	0	1	7	9	0	0	0	4	6	1	72
	336	65	?	5																												X
30	328	169	F	8	0.0	1.0	2.0	2.5	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	1.00	1.00	2.00	0	0	0	0	5	8	0	0	0	0	4	3	6
	329	85	?	8										0.00	0.00	0.00	0.00	0.00	0.00													X
31	322	119	F	5	0.0	0.0	0.0	0.0	1.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	7	8	9	0	0	0	3	6	1	116
	323	30	?	5										0.00	0.00	0.25	0.25	1.00	2.00	1	2	2	7	8	9	0	0	0	4	7		124
	324	74	?	5										0.00	0.00	0.25	0.25	1.00	2.00	0	1	2	7	8	9	0	0	0	4	7		121
	325	124	F	5	0.0	0.5	0.0	0.0	1.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	7	8	9	0	0	0	4	7	1	137
	326	97	F	5	0.0	0.0	0.0	0.0	1.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	7	8	9	0	0	0	4	6	1	130
	327	70	?	5										0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	7	8	9	0	0	0	4	6		62
32	320	172	F	8	0.0	0.0	0.0	0.5	1.0	3.0	3.0	4.0	4.0	0.00	0.00	0.25	0.25	0.25	1.00	0	0	1	7	7	9	0	0	4	5	7	1	0
	321	95	?	8																												X
33	182	34	M	3	0.0	0.0	0.0	1.0	1.5	3.0	4.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	6	7	9	9	9	9	1	4	5	5	7		1
	183	74	M	2.5	0.0	0.0	0.0	1.0	1.5	3.0	4.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	5	7	9	9	9	9	1	4	5	5	7		3
	184	59	M	2.5	0.0	0.0	1.0	1.0	1.5	3.0	4.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	5	7	9	9	9	9	1	4	5	5	7		4
	185	163	M	2.5	0.0	0.5	1.0	1.5	1.5	3.0	4.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	2	3	5	7	8	9	0	1	3	4	6		1
34	186	163	F	8	0.0	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	6	7	9	0	0	0	4	5	3	3
	187	148	F	8	0.0	0.0	0.0	0.5	1.5	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	6	7	9	0	0	0	3	5	3	2
35	188	129	M	5	1.0	2.0	2.0	3.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	1.00	2	2	3	6	8	9	0	0	5	5	6		7
	189	103	?	5										0.00	0.00	0.25	0.25	1.00	2.00	2	2	3	6	8	9	0	0	5	5	7		5
	190	109	M	5	1.0	1.0	2.0	3.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	2.00	2	2	3	6	8	9	1	3	5	5	7		11
	191	87	?	5										0.00	0.00	0.25	0.25	1.00	2.00	2	2	3	6	8	9	1	3	5	5	7		23
	192	99	M	5	1.0	1.0	2.0	2.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	2.00	2	2	2	6	8	9	1	3	5	5	7		2
36	312	53	M	5	1.0	1.0	1.0	2.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	1.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	0	5	7	1	6
	313	84	M	5	1.0	1.0	2.0	3.0	3.5	4.0	5.0	5.0	5.0	0.00	0.00	1.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	0	5	7	1	14
	314	234	M	5	1.0	2.5	3.0	3.5	3.5	4.0	5.0	5.0	5.0	0.00	0.00	1.00	2.00	2.00	2.00	0	0	2	5	8	9	0	0	1	4	5	1	19
	315	96	M	5	1.0	1.0	1.0	2.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	1.00	2.00	2.00	2.00	0	0	3	7	8	9	0	0	0	4	7	1	102
37	316	165	M	5	1.5	2.5	3.0	4.0	4.0	5.0	5.0	5.0	5.0	0.00	0.00	1.00	1.00	2.00	2.00	1	1	1	5	8	9	0	0	3	4	5		44
	317	109	?	5										0.00	0.00	1.00	1.00	2.00	2.00	1	1	1	5	8	9	0	0	3	4	7		3
38	310	131	F	7.5	0.0	0.0	0.5	1.0	2.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	0.25	1.00	0	0	0	0	6	8	0	0	0	3	6	2	0
	311	51	?	7.5										0.00	0.00	0.00	0.25	0.25	0.25	0	0	0	0	6	8	0	0	0	3	6	1	0
39	260	148	F	8	0.0	0.5	0.5	1.0	2.0	4.0	4.0	4.0	4.0	0.00	0.25	0.25	0.25	0.25	0.25	0	0	0	7	9	9	0	0	0	3	6	3	5
	261	166	F	7.5	0.0	0.0	1.0	1.0	2.0	4.0	4.0	4.0	4.0	0.00	0.25	0.25	0.25	0.25	1.00	0	0	0	7	9	9	0	0	0	3	6	3	0
40	193	130	M	8	2.0	3.0	4.0	4.0	4.0	4.0	5.0	5.0	5.0	0.00	0.25	0.25	1.00	2.00	2.00	0	0	0	6	7	9	0	0	0	3	5		0
	194	98	M	8	2.0	3.0	4.0	4.0	4.0	4.0	5.0	5.0	5.0	0.00	0.25	0.25	1.00	2.00	2.00	0	0	5	7	7	9	0	0	1	4	7		4
41	200	116	M	3	0.0	0.0	0.5	1.0	1.5	2.0	3.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	1	2	5	7	9	9	0	0	0	4	6		2
	203	68	M	3	0.0	0.0	0.5	1.0	1.0	2.0	3.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	7	9	9	0	0	0	4	6		2
	204	66	M	3	0.0	0.0	0.5	1.0	1.0	2.0	3.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	7	9	9	0	0	0	4	6		20
	205	25	?	4										0.25	0.25	1.00	2.00	2.00	2.00	1	2	5	7	9	9	0	1	0	4	6		2
	207	91	M	3	0.0	0.0	0.5	1.0	1.0	2.0	3.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	7	9	9	0	0	0	4	6		4
	208	89	M	3	0.0	0.0	0.5	1.0	1.0	2.0	3.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	7	9	9	0	0	0	4	6		0
	209	152	M	3	0.0	0.0	0.5	1.0	1.5	2.5	3.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	7	9	9	0	0	0	3	6		4
	210	169	M	3	0.0	0.0	0.5	1.0	2.0	3.0	3.0	3.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	5	7	9	9	0	0	0	3	6		2
	214	68	?	2.5										0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	7	9	9	0	0	0	5	6		0
42	201	47	M	2	0.0	0.0	0.0	0.0	0.5	1.0	2.0	2.5	3.0	0.25	0.25	1.00	2.00	2.00	2.00	1	2	6	7	8	9	0	1	3	4	6		0
	211	88	M	2.5	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	0.00	0.25	0.50	1.00	1.00	2.00	1	1	5	7	9	9	0	0	0	4	6		0
43	196	74	F	2	0.0	0.0	0.0	0.0	1.0	3.0	3.0	3.5	4.0	0.25	0.25	1.00	1.00	2.00	2.00	2	3	6	7	8	9	1	3	3	4	6		0
	197	102	F	2	0.0	0.0	0.0	1.0	1.0	3.0	3.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	2	3	6	7	8	9	0	3	3	4	6		1
	198	120	F	2	0.0	0.0	0.0	0.5	1.0	3.0	3.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	2	3	6	7	8	9	0	3	3	4	6		2
	199	130	F	2	0.0	0.0	0.0	0.5	1.0	3.0	3.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	2	3	6	7	8	9	0	3	3	4	6		0
	202	66	F	2.5	0.0	0.0	0.0	0.5	1.0	3.0	3.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	1	2	6	7	8	9	0	1	3	4	6		0

Continued - Table 4-25. Hypothesized clone groupings based on sex, leaf shape, and phenology similarities.

	ID#	CBH	Sex	Spec	Flowering									Leaf Flush						Senescence						Leaf Drop					BSac.	Galls
44	215	106	M	2	0.0	0.5	1.0	1.0	1.5	3.0	4.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	5	7	9	9	0	0	0	4	6		2
	216	130	M	2	0.0	0.5	1.0	1.0	1.5	3.0	4.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	5	7	9	9	0	0	0	4	6		0
	219	147	M	2	0.0	0.5	1.0	1.0	1.5	3.0	3.0	4.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	0	4	7	9	9	0	0	0	3	6		0
45	220	48	F	3.5	0.0	0.5	1.5	2.0	3.0	4.0	4.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	2	5	9	9	9	9	0	1	5	7	7		2
	221	143	F	3.5	0.0	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	5	5	7	9	9	9	0	1	4	5	7		78
	222	15	?	3.5																												X
46	248	28	?	5										0.00	0.00	0.25	1.00	1.00	2.00	0	0	0	3	6	9	0	0	0	0	4		4
	249	35	M	5	0.0	0.0	0.0	0.0	1.0	3.0	3.0	4.0	4.0	0.00	0.00	0.25	1.00	1.00	2.00	0	0	0	3	6	9	0	0	0	0	4		1
	257	27	M	5	0.0	0.0	0.0	0.5	1.0	3.0	3.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	2	6	9	0	0	0	1	4		1
	393	22	M	5	0.0	0.0	0.0	0.5	1.0	3.0	3.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	2	6	9	0	0	0	1	4		13
47	250	27	?	5										0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	7	9	9	0	0	3	5	7		6
	251	29	?	5										0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	7	9	9	0	0	3	5	7		0
	252	21	?	5										0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	7	9	9	0	0	3	7	7		13
	253	25	?	5										0.00	0.00	0.25	0.25	1.00	2.00	0	0	1	7	9	9	0	0	3	5	7		0
48	254	73	?	8										0.00	0.00	0.00	0.25	0.25	1.00	0	0	0	0	6	9	0	0	0	1	5	1	1
	255	139	M	8	1.5	2.0	2.0	3.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	0.00	0.25	0.25	1.00	0	0	0	0	6	9	0	0	0	3	4	2	3
	263	93	M	8	1.5	1.5	2.0	3.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	0.00	0.25	0.25	0.25	0	0	0	7	6	9	0	0	1	5	7	3	0
49	244	177	M	8	1.5	2.0	3.0	3.0	4.0	5.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	6	9	0	0	0	3	3	2	0
	245	148	M	8	1.5	2.0	3.0	3.0	4.0	5.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	0	6	9	0	0	0	3	4	2	2
	258	190	M	8	2.0	2.0	3.0	3.0	4.0	4.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	6	9	0	0	0	3	4	3	5
50	246	189	F	5	0.0	0.0	1.0	1.0	2.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	8	9	0	0	0	3	6	2	1
	247	142	F	5	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	8	9	0	0	0	3	6	2	0
51	240	232	F	7	0.5	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	0	7	8	0	0	0	0	3	3	0
	241	178	?	7										0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	0	7	8	0	0	0	0	3	3	1
	242	196	F	7	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	0	7	8	0	0	0	0	3	3	0
	243	204	F	8	0.0	1.0	1.5	2.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	0	7	0	0	0	0	3	3	1
52	265	164	F	5	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	2	6	8	9	0	0	0	3	5		57
	266	127	F	5	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	2	5	8	9	0	0	0	3	5		0
	267	54	?	5																												X
	272	127	F	5	0.0	1.0	2.0	2.5	3.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	0	0	8	9	0	0	0	4	7	1	48
	275	66	F	5																												0
53	279	29	M	2.5	0.0	0.0	0.0	0.5	1.0	2.0	2.0	3.0	4.0	0.00	0.25	0.25	1.00	2.00	2.00	1	1	6	7	9	9	0	1	3	4	6		0
	280	21	?	2										0.00	0.25	0.25	1.00	2.00	2.00	2	2	5	7	9	9	1	1	4	5	6		0
54	264	261	F	8	1.0	1.0	2.5	3.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	6	9	0	0	0	3	5	2	4
	304	172	F	8	1.0	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	6	8	0	0	0	3	4	3	16
	305	187	F	8	1.0	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	6	8	0	0	0	3	4	3	0
	341	183	F	8	0.0	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	6	6	0	0	0	0	4	2	5
	344	207	F	8	0.0	1.0	1.5	2.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	6	8	0	0	0	0	3	3	0
55	343	181	F	5	0.0	1.0	1.5	2.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	1.00	2.00	2.00	2.00	2	4	5	7	9	9	0	1	3	5	6		4
	373	144	F	5.5	1.0	1.0	1.5	2.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	1	1	4	7	8	9	0	0	3	3	6	2	0
	374	178	F	5.5	1.0	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	1.00	1.00	2.00	2.00	0	0	4	6	8	9	0	0	0	3	5	3	4
	375	185	F	5.5	0.0	0.5	0.5	0.5	1.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	4	7	8	9	0	0	3	5	7	2	1
	376	20	?	5										0.00	0.00	0.25	0.25	1.00	1.00	1	1	2	6	8	9	0	0	0	5	6		0
	394	17	?	5										0.00	0.00	0.25	0.25	1.00	1.00	1	1	2	6	8	9	0	0	0	5	6		0
56	345	19	?	5																												X
	348	18	?	5										0.00	0.25	1.00	1.00	2.00	2.00	1	1	2	7	9	9	0	4	5	7	7		1
	349	25	?	5										0.00	0.25	1.00	1.00	2.00	2.00	1	1	2	7	9	9	0	4	5	5	7		0
57	306	129	M	5.5	2.0	3.0	3.5	4.0	4.0	4.0	5.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	2	2	2	7	9	9	0	0	4	5	7		19
	307	152	M	5.5	2.0	3.0	3.5	4.0	4.0	4.0	5.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	2	2	2	7	9	9	0	0	3	5	7		1
	308	172	M	5.5	2.0	3.0	3.5	4.0	4.0	4.0	5.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	2	2	2	7	9	9	0	0	3	5	7		26
	309	107	?	5.5										0.00	0.25	1.00	2.00	2.00	2.00	2	4	4	7	9	9	1	3	3	5	7		31
58	281	70	M	3.5	0.0	1.0	1.0	2.0	2.5	4.0	5.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	5	6	7	9	9	1	1	1	3	6		2
	282	103	M	3.5	1.0	1.0	1.0	2.0	2.5	4.0	5.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	2	5	7	9	9	0	1	1	4	6		11
59	283	186	M	5.5	1.0	2.0	2.0	3.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	1.00	1.00	2.00	2.00	0	1	2	6	8	9	0	0	1	4	6		0
	284	156	M	5.5	1.0	2.0	2.0	3.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	1.00	1.00	2.00	2.00	0	1	2	6	8	9	0	0	1	4	6		2

Continued - Table 4-25. Hypothesized clone groupings based on sex, leaf shape, and phenology similarities.

	ID#	CBH	Sex	Spec	Flowering									Leaf Flush						Senescence						Leaf Drop					RSuc.	Galls
60	286	86	?	5.5																												X
	287	165	F	5.5	0.0	0.5	1.0	3.0	3.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	1	3	6	7	8	9	0	0	4	5	6		3
	288	98	?	5										0.00	0.25	1.00	2.00	2.00	2.00													X
	289	92	?	5																												X
61	356	47	?	5																												X
	357	47	?	5																												X
	358	39	?	5																												X
	359	82	F	5	0.0	0.0	0.0	0.0	1.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	1.00	0	1	2	7	8	9	0	0	3	4	6		32
	360	218	F	5	0.0	0.0	0.0	1.0	1.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	6	8	9	0	0	3	3	5	2	0
	361	95	F	5	0.0	0.0	0.0	0.0	1.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	2	7	8	9	0	0	3	4	6		64
	362	104	F	5	0.0	0.0	0.0	0.0	1.0	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	2	6	8	9	0	0	3	4	6		84
	363	243	F	5	0.0	0.0	0.0	1.0	1.5	3.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	5	8	9	0	0	0	4	5	3	39
62	369	37	?	3																												X
	370	26	?	2.5																												X
63	378	49	?	3																												X
	379	25	?	3																												X
64	364	163	F	5	1.5	2.0	3.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	3	6		146
	365	47	F	5	1.5	2.0	3.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.25	1.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	3	6		91
65	295	93	M	5	1.5	2.0	2.0	3.0	3.5	4.0	5.0	5.0	5.0	0.00	0.25	0.25	0.25	1.00	1.00	0	0	1	5	8	9	0	0	0	3	6		89
	296	72	M	5	1.5	2.0	2.0	3.0	3.5	4.0	5.0	5.0	5.0	0.00	0.25	0.25	1.00	2.00	2.00	0	0	1	6	8	9	0	0	0	4	6		99
66	292	53	M	5	2.0	3.0	4.0	4.0	4.0	4.0	5.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	0	0	0	8	9	0	0	0	3	6	1	27
	293	29	?	5										0.25	0.25	1.00	2.00	2.00	2.00	0	0	0	0	8	9	0	0	0	3	6	1	0
	294	143	M	5	2.5	3.0	4.0	4.0	4.0	4.0	5.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	0	0	0	0	8	9	0	0	0	3	5	1	0
67	299	132	?	5										0.00	0.25	0.25	1.00	2.00	2.00	0	0	0	0	5	5	0	0	0	4	5		20
	300	192	?	5										0.00	0.25	0.25	1.00	1.00	2.00	0	0	0	0	5	5	0	0	0	3	5		12

Continued - Table 4-25. Hypothesized clone groupings based on sex, leaf shape, and phenology similarities.

	ID#	CBH	Sex	Spec	Flowering									Leaf Flush						Senescence						Leaf Drop					BSac.	Galls
Single:	1	237	F	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	2.0	0.00	0.00	0.00	0.25	1.00	1.00	1	2	5	7	9	9	0	0	2	4	6		0
	51	138	F	3.5	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	3	7	9	9	0	0	2	5	7		4
	76	62	F	1	0.0	0.0	0.5	1.0	2.5	3.5	4.0	4.0	4.0	0.25	1.00	2.00	2.00	2.00	2.00	2	5	7	7	8	9	4	5	5	5	6		0
	90	228	M	6.5																												X
	121	31	?	1										0.25	0.25	1.00	2.00	2.00	2.00	2	2	2	7	8	9	0	0	2	5	6		0
	122	135	?	3.5																												X
	125	108	M	5	1.0	1.0	2.0	3.0	4.0	5.0	5.0	5.0	5.0	0.25	0.25	0.25	1.00	2.00	2.00													20
	131	81	?	3.5																												X
	136	109	M	8	2.0	2.0	3.0	3.0	4.0	5.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	0	6	9	0	0	0	1	5	3	3
	158	106	?	2										0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	6	8	9	0	0	0	4	7		2
	177	88	M	8	1.0	2.0	3.0	3.0	4.0	4.0	5.0	5.0	5.0	0.00	0.25	0.25	0.25	1.00	1.00	0	0	0	6	6	9	0	0	0	3	5		3
	195	88	F	1.5	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	2	5	6	7	9	9	0	3	4	5	7		0
	213	130	F	2.5	0.0	0.0	0.0	0.0	0.0	0.0	1.0	3.0	3.0	0.00	0.25	0.25	0.25	1.00	2.00	0	0	5	7	9	9	0	0	0	5	6		3
	217	115	M	8	1.0	1.0	1.0	2.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	0	0	6	9	0	0	0	3	4	2	1
	256	118	M	5	0.0	0.5	1.0	1.5	2.0	3.0	4.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	0	0	0	7	0	0	0	0	4	2	4
	259	154	M	7.5	0.0	0.5	1.0	2.0	3.0	4.0	5.0	5.0	5.0	0.00	0.00	0.00	0.25	0.25	0.25	0	0	5	7	9	9	0	0	0	4	7	1	2
	262	139	M	8	1.5	2.0	3.0	4.0	4.0	4.0	5.0	5.0	5.0	0.25	0.25	0.25	0.25	1.00	2.00	0	0	0	0	6	8	0	0	0	3	4	2	0
	268	114	M	3.5	0.0	0.5	1.0	1.5	1.5	3.0	4.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	5	5	6	7	8	9	0	1	4	4	6		0
	269	105	F	8	0.0	0.0	0.0	0.0	1.0	2.0	3.0	4.0	4.0	0.00	0.25	0.25	0.25	1.00	2.00													X
	270	128	M	5	2.0	3.0	3.5	4.0	4.0	5.0	5.0	5.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	2	2	3	7	9	9	0	0	1	5	6	1	113
	271	71	M	5.5	2.0	2.0	3.0	3.5	4.0	5.0	5.0	5.0	5.0	0.00	0.25	0.25	1.00	1.00	2.00	2	5	5	7	8	9	0	0	3	5	7		107
	273	109	F	2	0.0	0.0	0.0	0.0	0.0	1.0	2.0	3.0	3.0	0.00	0.25	0.25	1.00	1.00	2.00	2	3	4	7	8	9	1	3	4	4	6		0
	274	209	M	5	1.0	1.0	2.0	3.0	4.0	5.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	1.00	0	0	2	5	8	9	0	0	1	3	6		127
	276	158	F	3	0.0	0.0	0.0	0.5	1.0	2.0	3.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	0	0	2	6	7	9	0	0	0	3	6		2
	278	54	?	5										0.00	0.00	0.00	0.25	1.00	2.00	1	2	4	6	8	9	0	0	3	5	7		X
	285	86	M	2.5	0.0	0.5	1.0	1.0	1.5	2.0	3.0	4.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	3	7	9	9	0	0	0	4	6		4
	290	200	M	5.5																												131
	291	119	M	2.5	0.0	1.0	1.0	1.0	2.0	3.0	4.0	5.0	5.0	0.25	1.00	2.00	2.00	2.00	2.00	0	0	1	6	8	8	0	0	0	3	4	1	0
	297	89	F	2	0.0	0.0	0.0	0.0	1.0	3.0	4.0	4.0	4.0	0.00	0.25	0.25	0.25	1.00	2.00	0	0	5	7	8	9	0	0	1	4	7		5
	298	23	?	5										0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	7	8	9	0	0	1	5	7		0
	301	161	M	5.5	3.0	3.5	4.0	4.0	4.0	5.0	5.0	5.0	5.0	0.00	0.25	0.25	1.00	1.00	2.00	0	1	1	5	8	9	0	0	0	4	6		1
	302	88	F	2	0.0	0.0	0.0	1.0	1.5	3.0	4.0	4.0	4.0	0.25	0.25	1.00	2.00	2.00	2.00	1	5	7	9	9	9	0	1	4	5	6		11
	303	23	?	5.5										0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	7	9	9	0	1	4	5	7		33
	318	184	F	5	0.0	0.5	1.0	2.0	3.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	1.00	2.00	2.00	1	1	1	5	8	9	0	1	4	4	7		11
	319	128	F	8	1.0	2.0	3.0	3.0	4.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	1.00	2.00	2.00	0	0	0	0	7	8	0	0	0	3	4	2	4
	337	137	M	8	1.0	2.0	2.5	3.0	4.0	4.0	5.0	5.0	5.0	0.00	0.00	0.25	1.00	1.00	1.00	0	0	0	0	6	8	0	0	0	3	4	3	0
	342	202	M	5	2.5	3.0	3.5	3.5	4.0	5.0	5.0	5.0	5.0	0.25	0.25	1.00	1.00	2.00	2.00	2	4	4	7	9	9	0	0	3	5	6	3	2
	346	247	F	8																												11
	347	141	F	8	0.0	0.5	0.5	1.0	2.0	4.0	4.0	4.0	4.0	0.00	0.00	0.25	0.25	0.25	1.00	0	0	0	0	6	8	0	0	0	0	4	3	1
	350	122	M	8	2.0	2.0	2.5	3.0	4.0	4.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	0.25	1.00	0	0	0	0	6	9	0	0	0	3	4	1	4
	355	198	M	5.5	1.5	1.5	2.0	2.5	3.0	4.0	5.0	5.0	5.0	0.00	0.00	0.25	0.25	1.00	2.00	0	0	2	6	8	8	0	0	0	4	6	1	11
	366	26	?	2										0.25	0.25	1.00	2.00	2.00	2.00													0
	367	16	M	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.25	1.00	2.00	2.00	2.00	2.00	1	1	1	1	6	7	0	0	0	4	6		114
	368	23	M	2	0.0	0.0	1.0	1.0	2.0	3.0	4.0	5.0	5.0	0.25	0.25	1.00	2.00	2.00	2.00	1	1	2	7	9	9	0	1	5	5	6		1
	371	61	M	5.5	3.0	3.0	3.5	4.0	4.0	5.0	5.0	5.0	5.0	0.00	0.00	1.00	1.00	1.00	2.00	2	2	4	7	8	9	0	0	0	4	5		X
	372	31	?	5																												X
	377	12	?	5																												X
	391	25	M	5	0.0	1.0	1.0	1.0	2.0	3.0	4.0	4.0	5.0	0.00	0.25	1.00	2.00	2.00	2.00	1	1	5	7	8	9	0	0	3	5	7		10

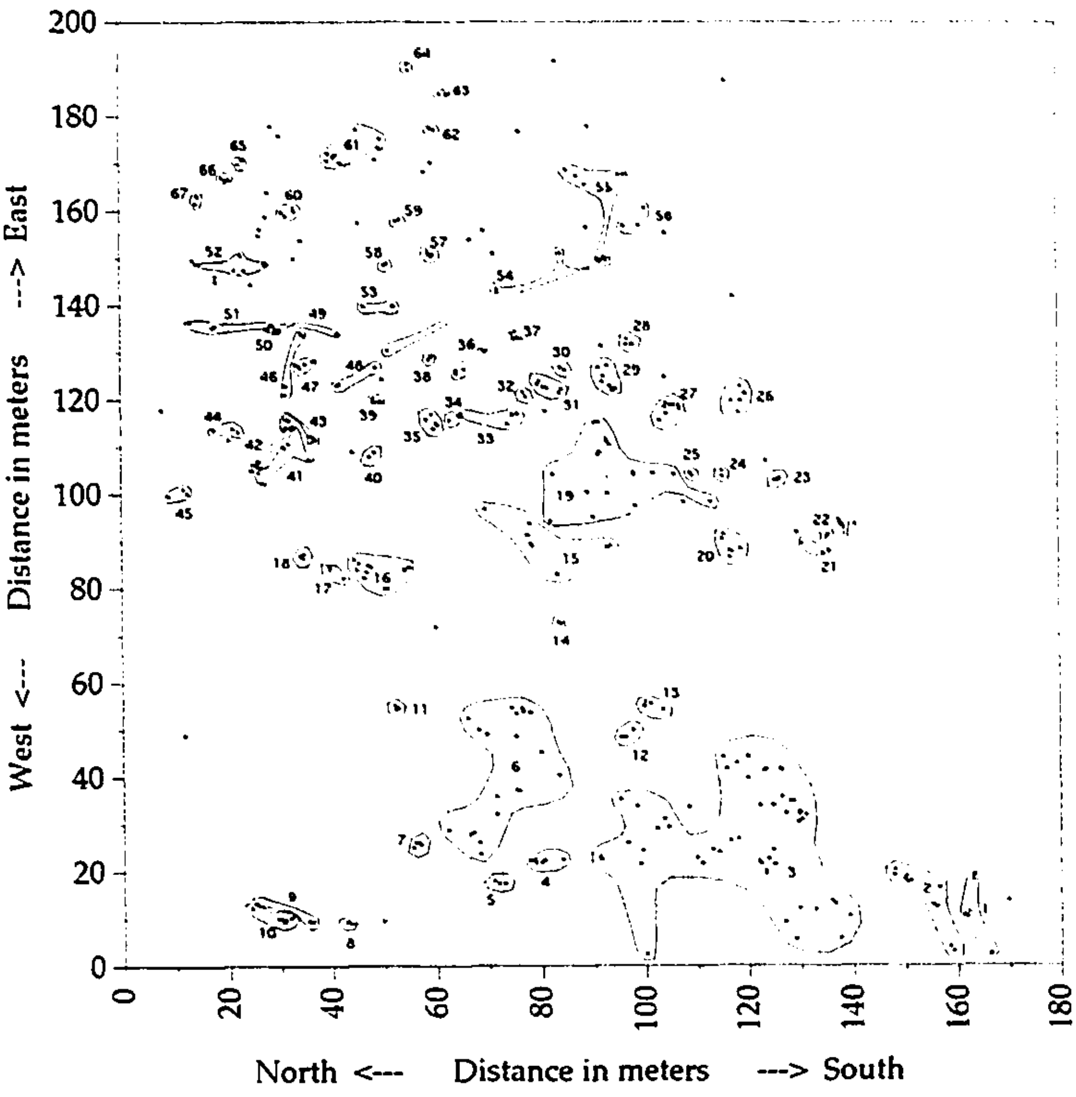


Figure 4-41. Spatial distribution of single trunks (n=48), and hypothesized clone groups (n=67), labelled with their clone identification numbers.

The last remaining set of characteristics are the leaf measurements. Variation in leaf dimensions as summarized by general leaf shape has been used to distinguish differences in species composition. These measurements can also aid investigation of variation at an individual, or clonal level. The potential for leaf measurement variability among the ramets of a clone would be expected to surpass that for a single tree. The additional variability could originate from both environmental and maturity-related effects. Since siblings represent the greatest similarity possible among non-clonally related individuals, it is expected that leaf dimensions compared among ramets will be more similar than those among half-siblings. The half-siblings available for analysis were under one year of age, and it is suspected that their leaf measurements are only generally comparable to those of the mature population. The blade width and petiole length for every ramet of each putative clone is illustrated in Fig. 4-42 for cautious comparison with those from the half-sibling groups in Fig. 4-39. While some clones had a greater degree of variation than others, within clone variation in the majority of cases was comparable to, or less than, that detected between the half-siblings. Due to the difficulties of interpreting variation in the immature leaf measurements, it was unclear how within-clone leaf measurement variability compared to that found among half-siblings.

By focusing on the clustered distribution of phenotypic characteristics in the population, it has been possible to detect spatially associated groups of similar trees. The characteristics found to be most effective in tracing these patterns, listed in order of utility, were; sex, species-type, phenology, spatial distribution, gall abundance, and close spacing of trunks. Based on the heritability of traits and spatial clustering, it is believed that the hypothesized groupings represent clonally related individuals.

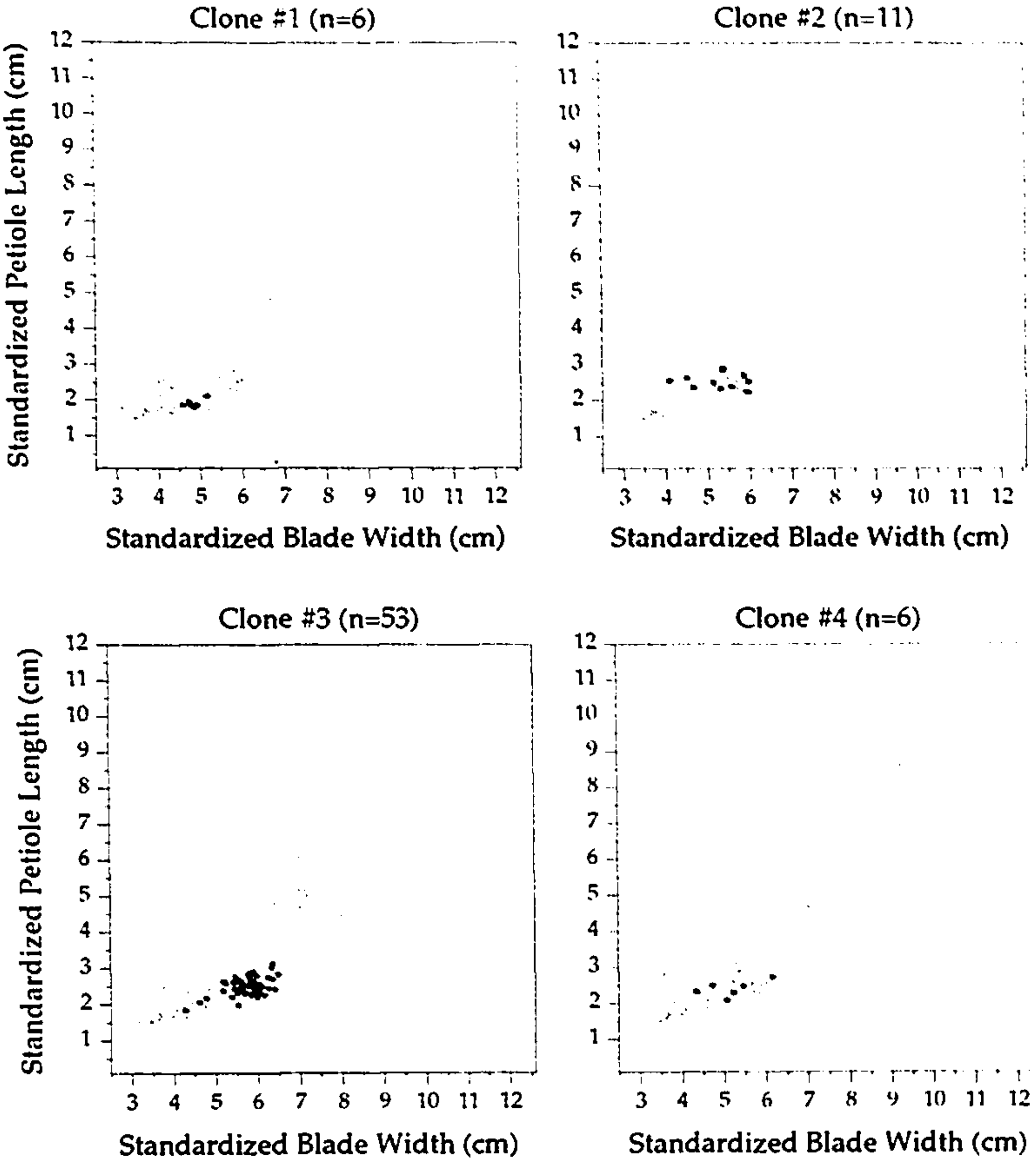
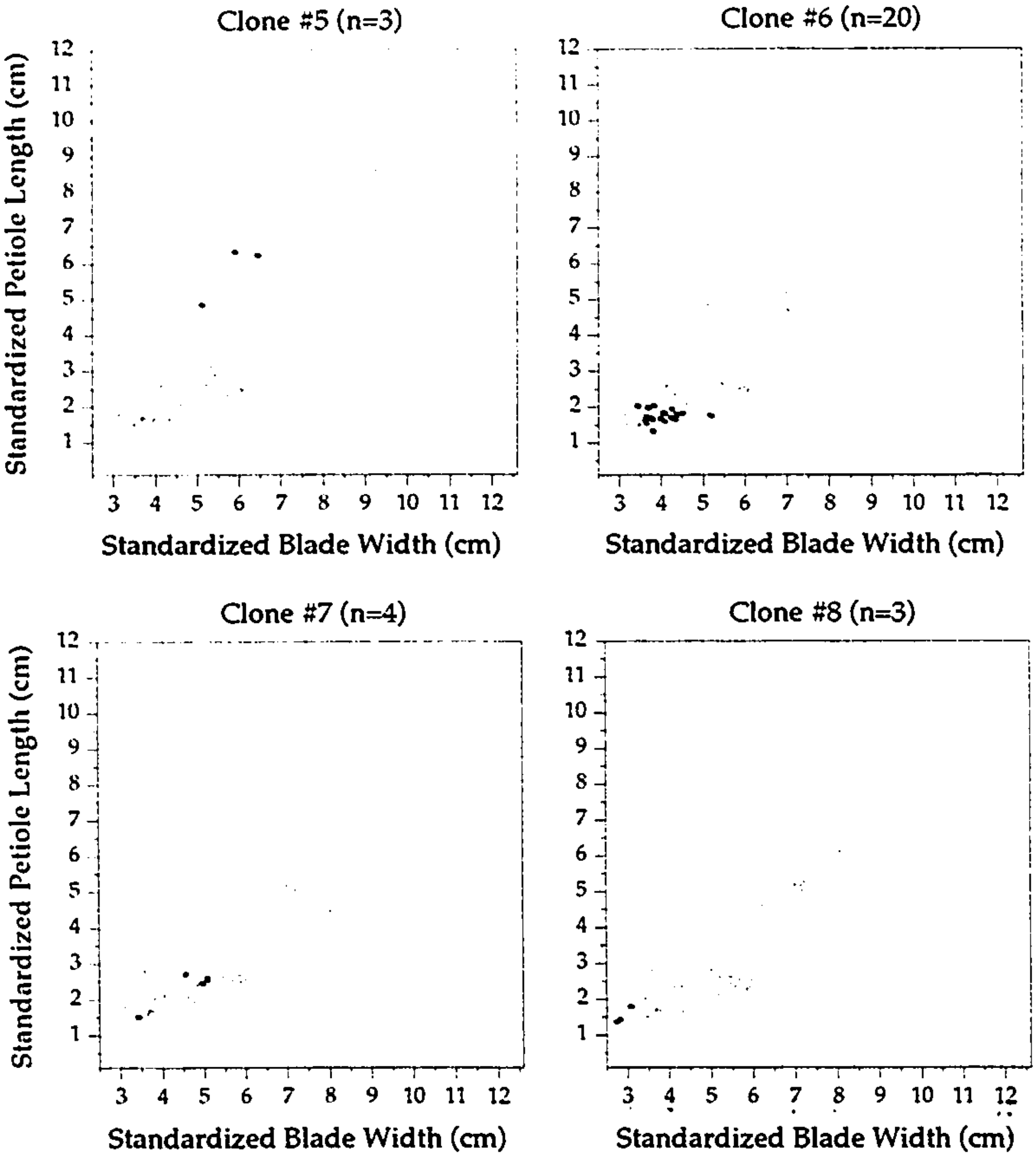
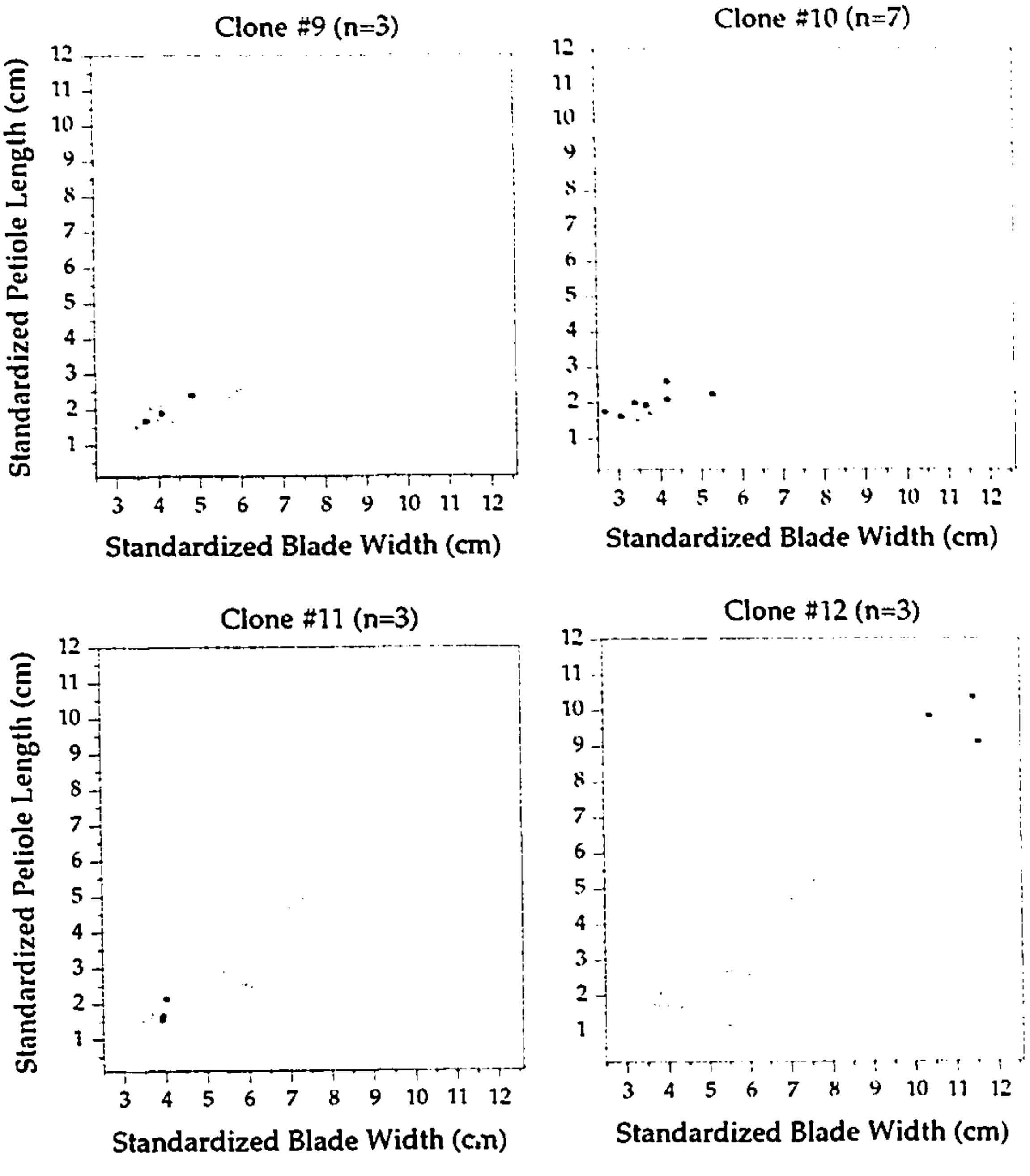


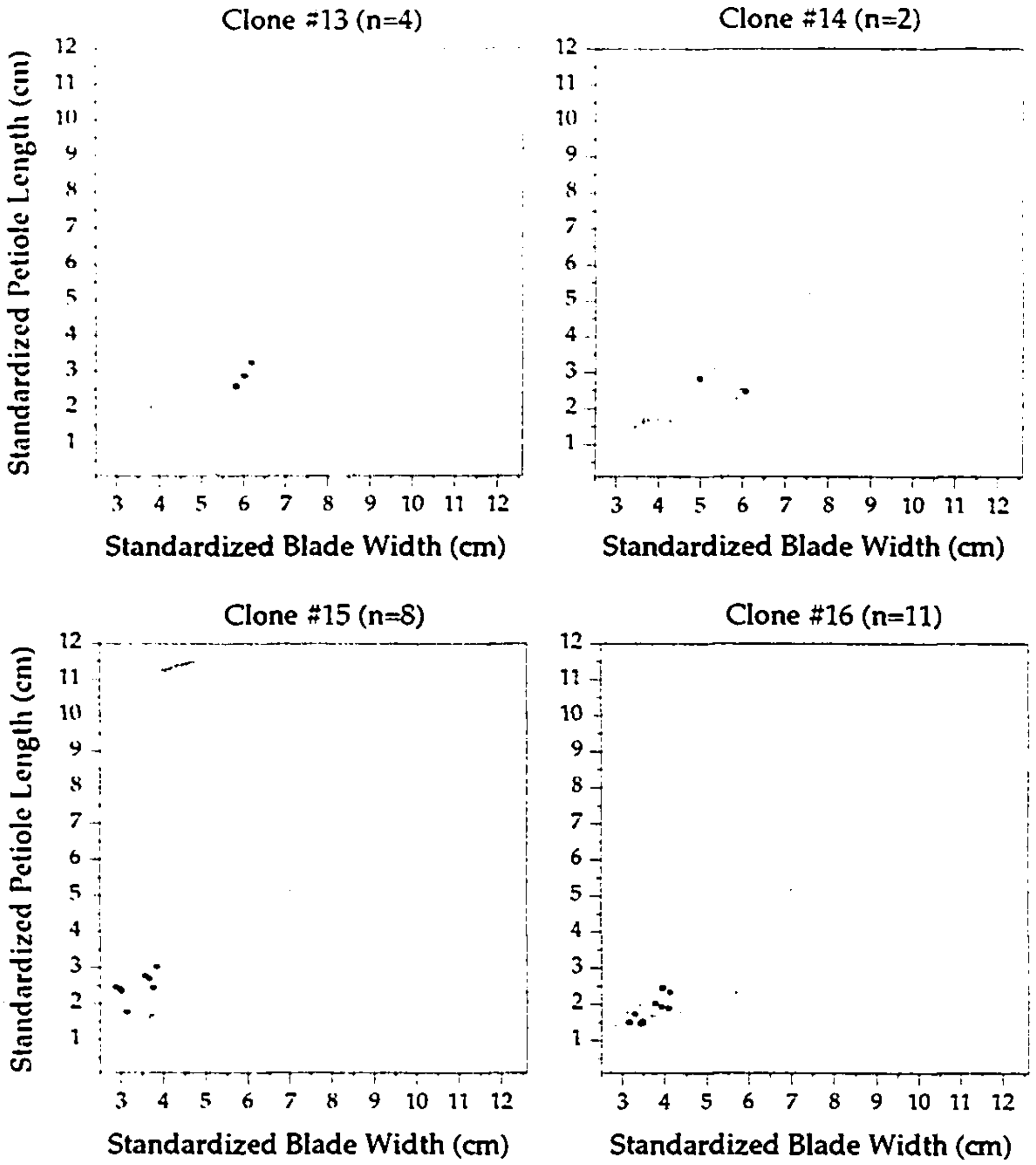
Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on the study site (N=391).



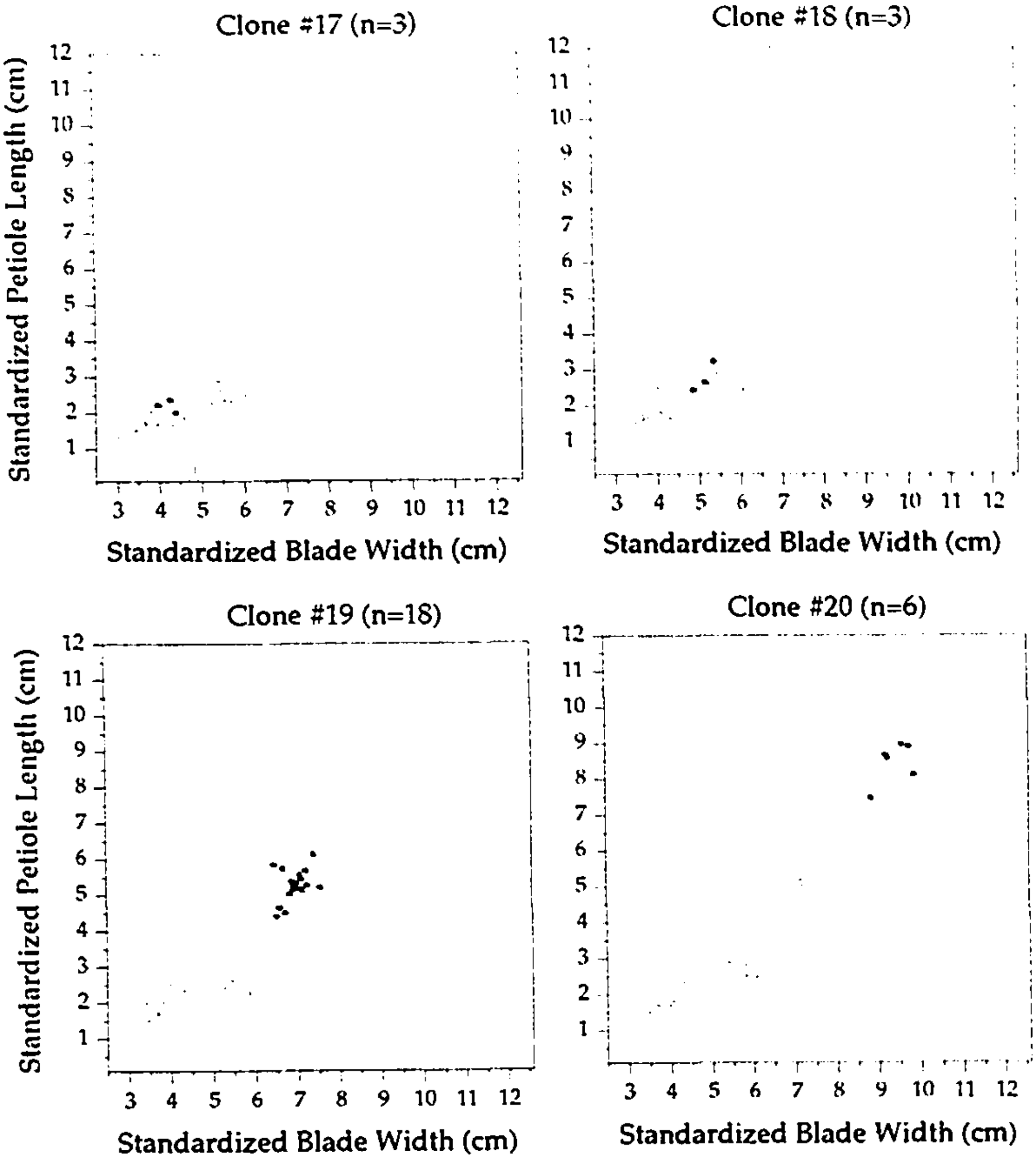
Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



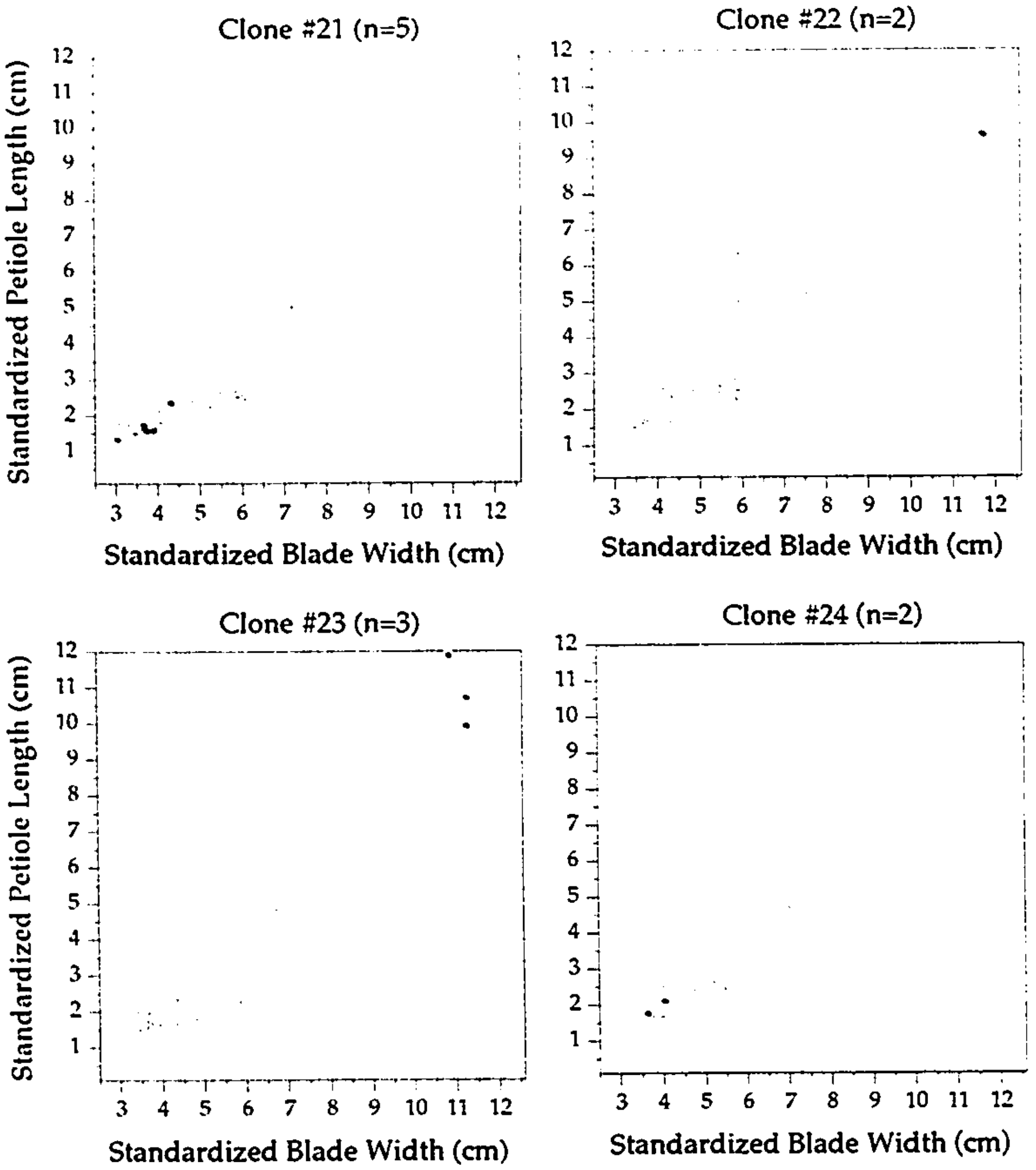
Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



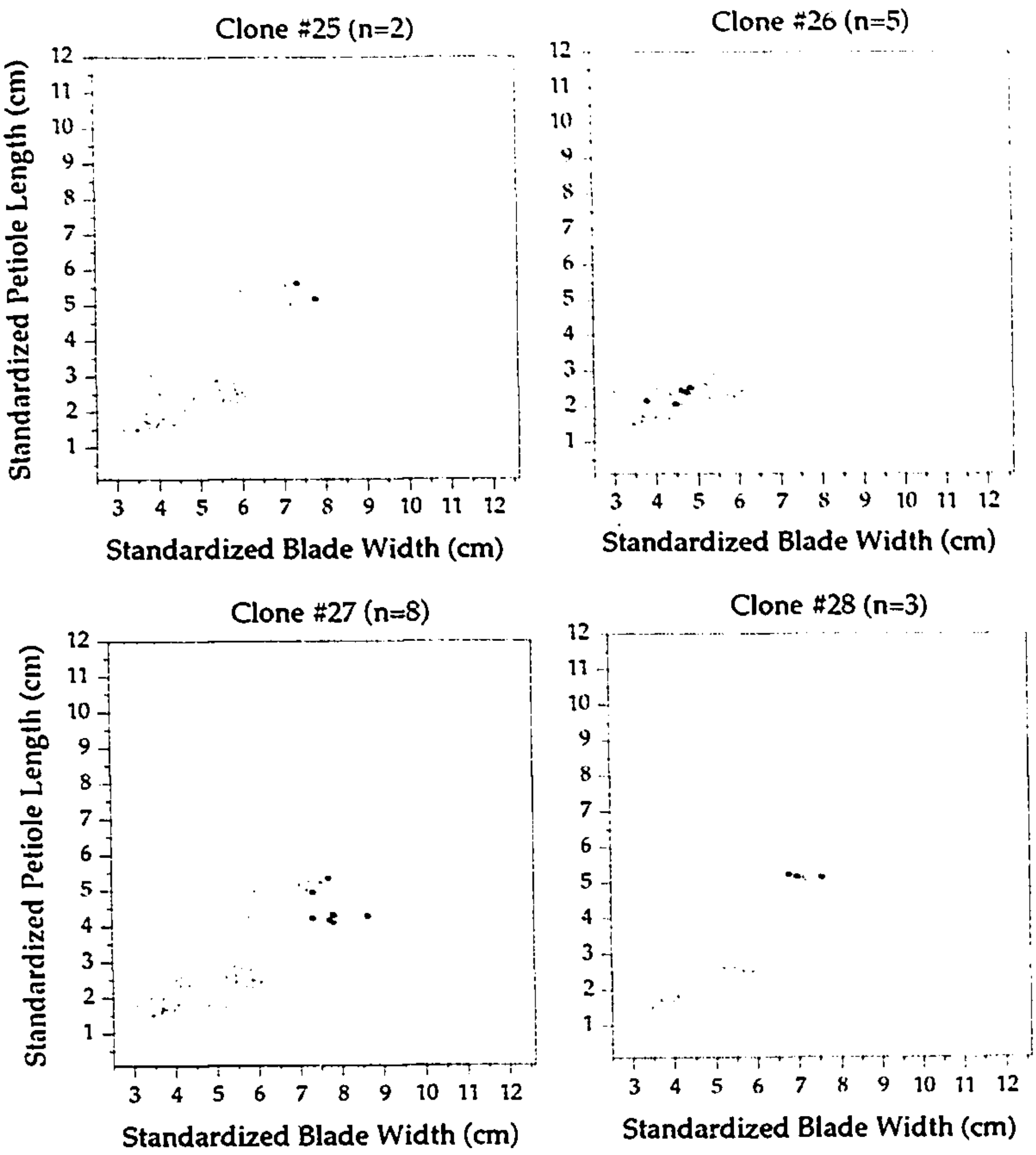
Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



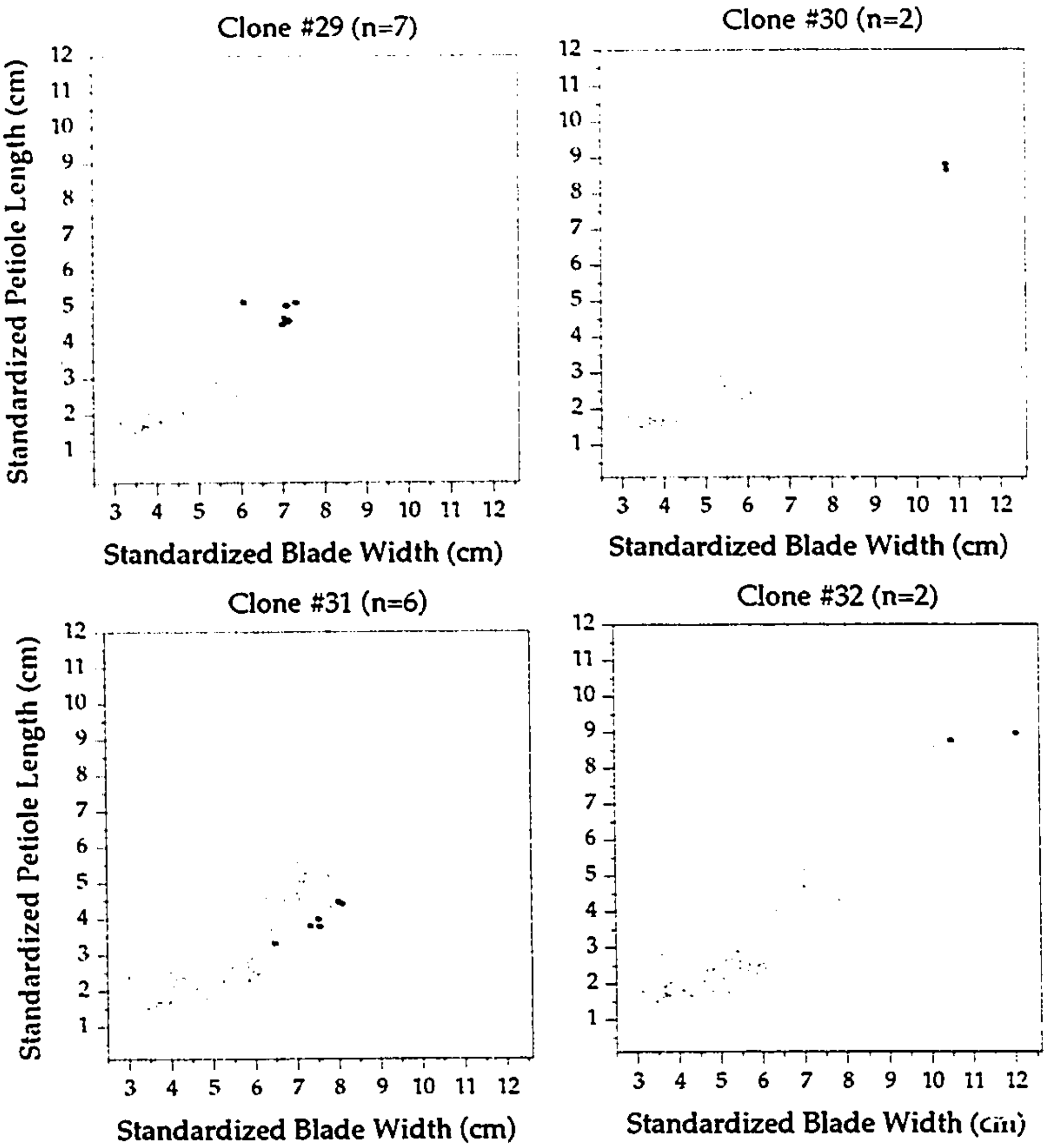
Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



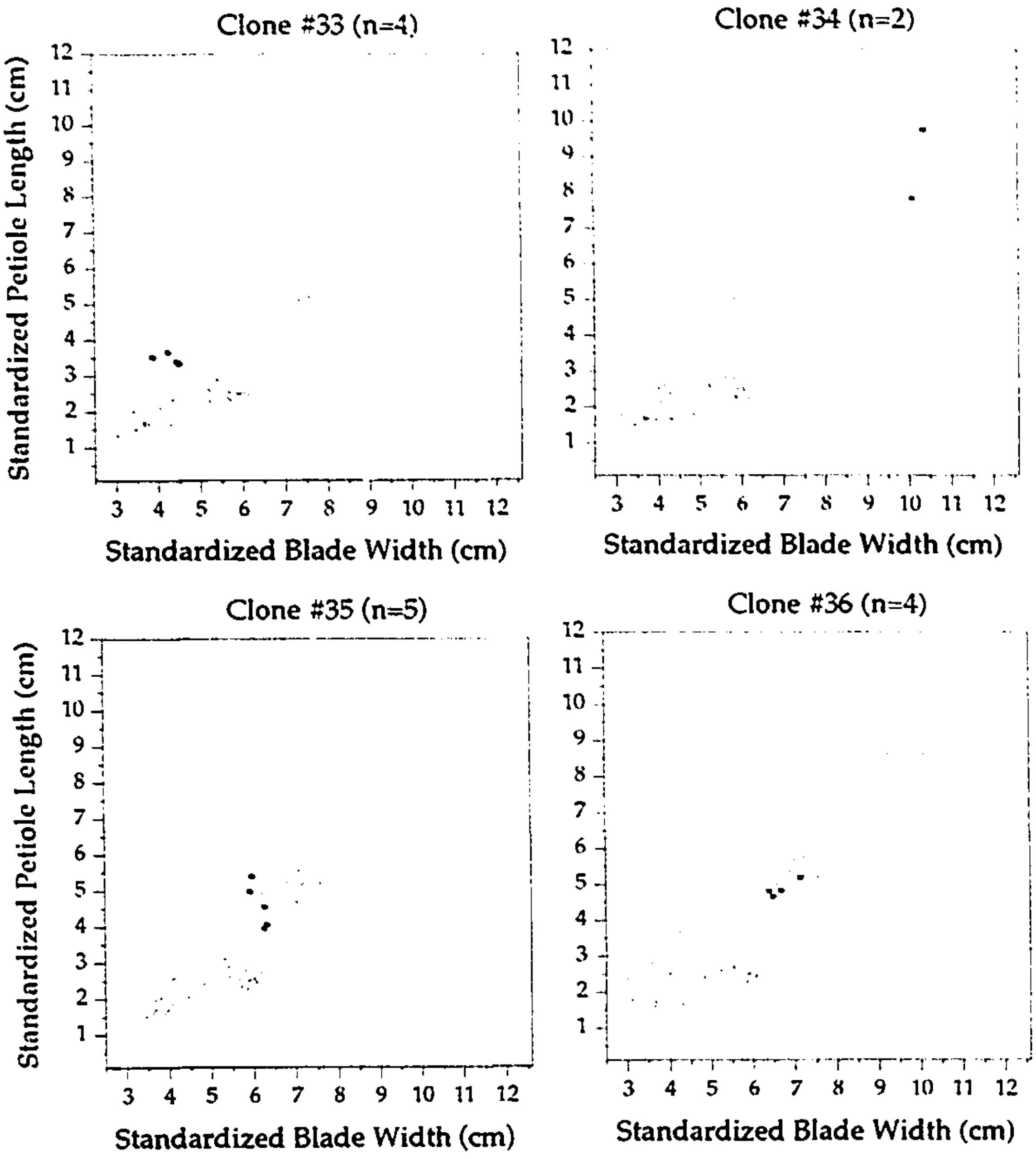
Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



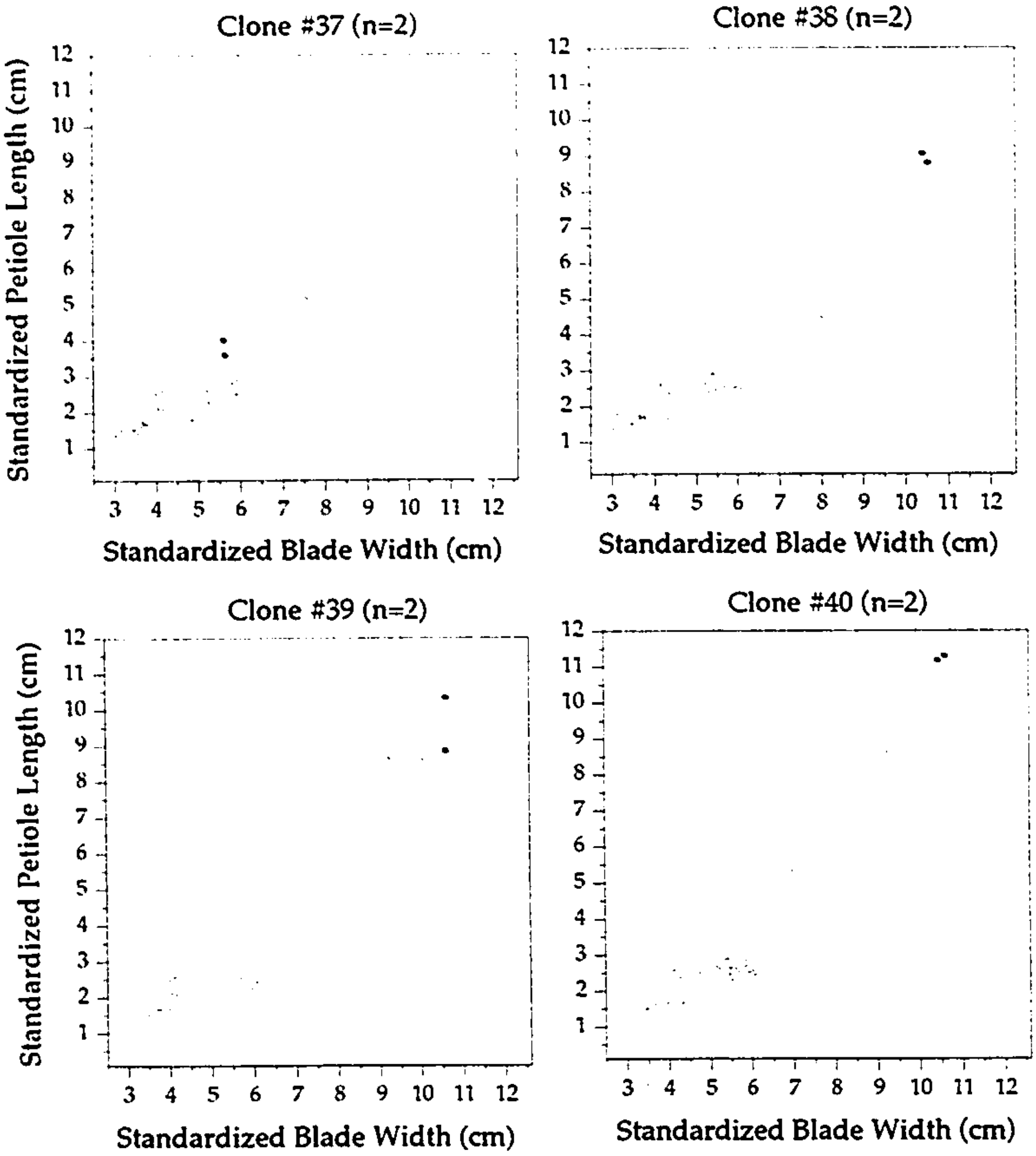
Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



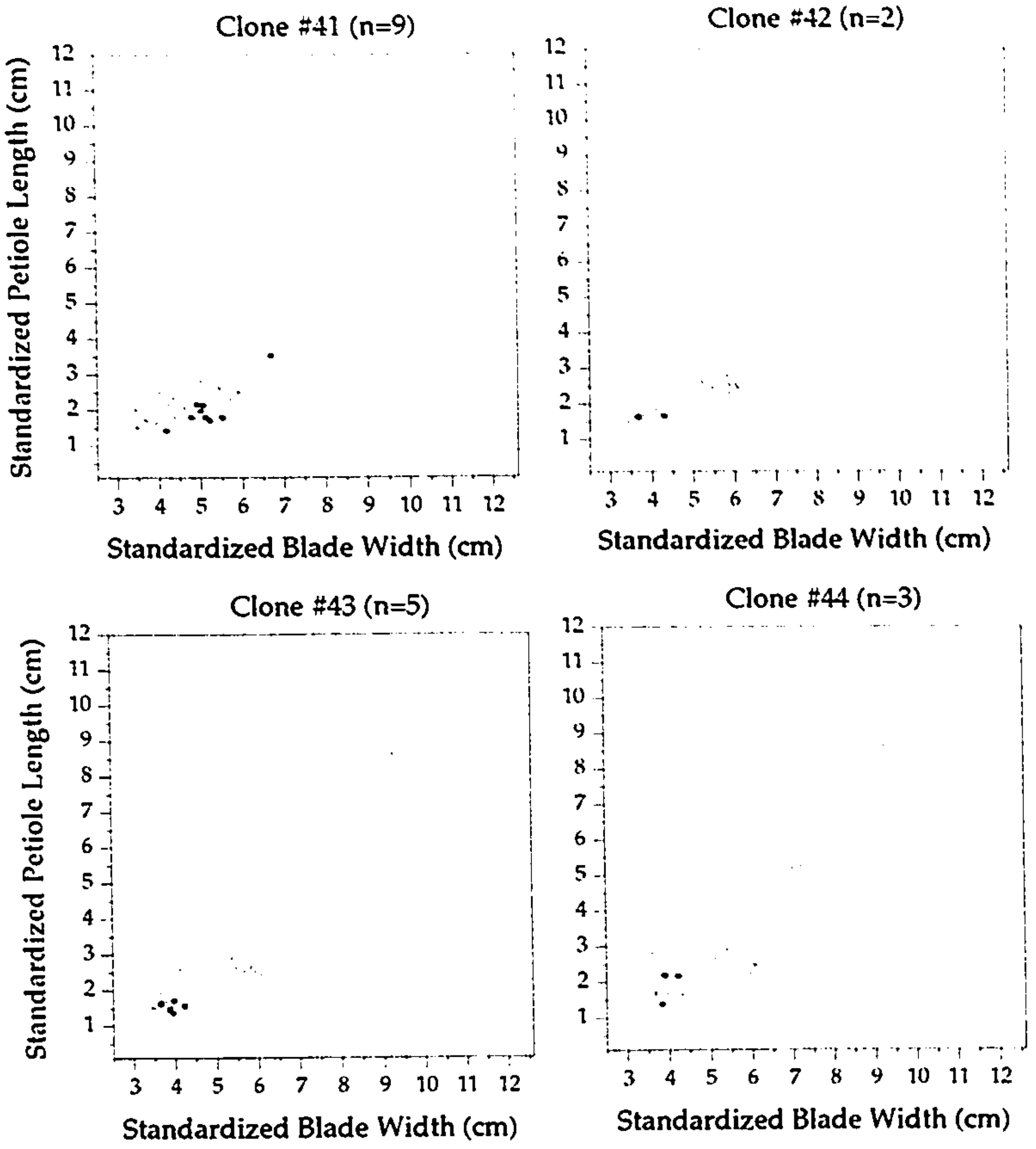
Clone #37 (n=2)

Clone #38 (n=2)

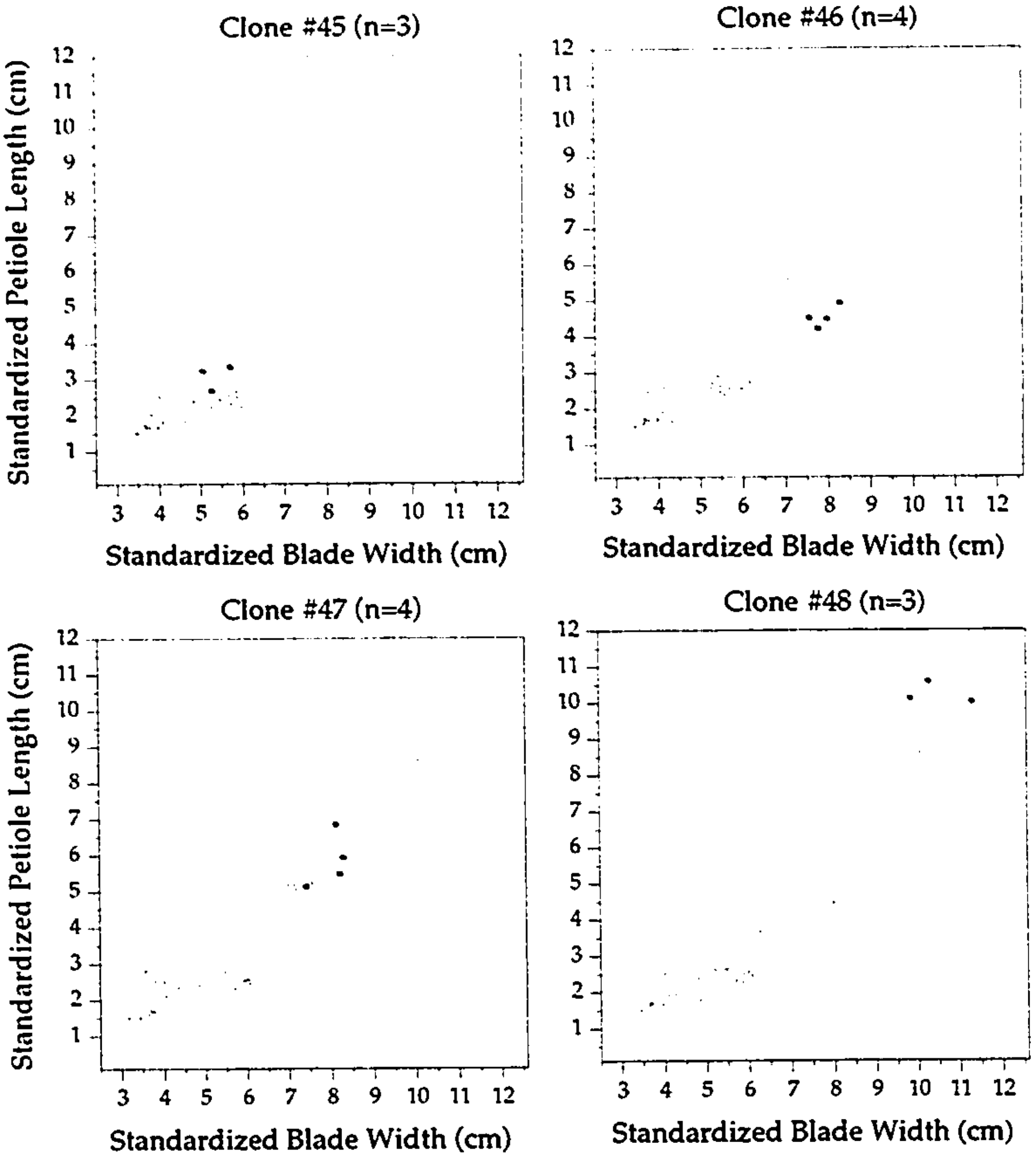
Clone #39 (n=2)

Clone #40 (n=2)

Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



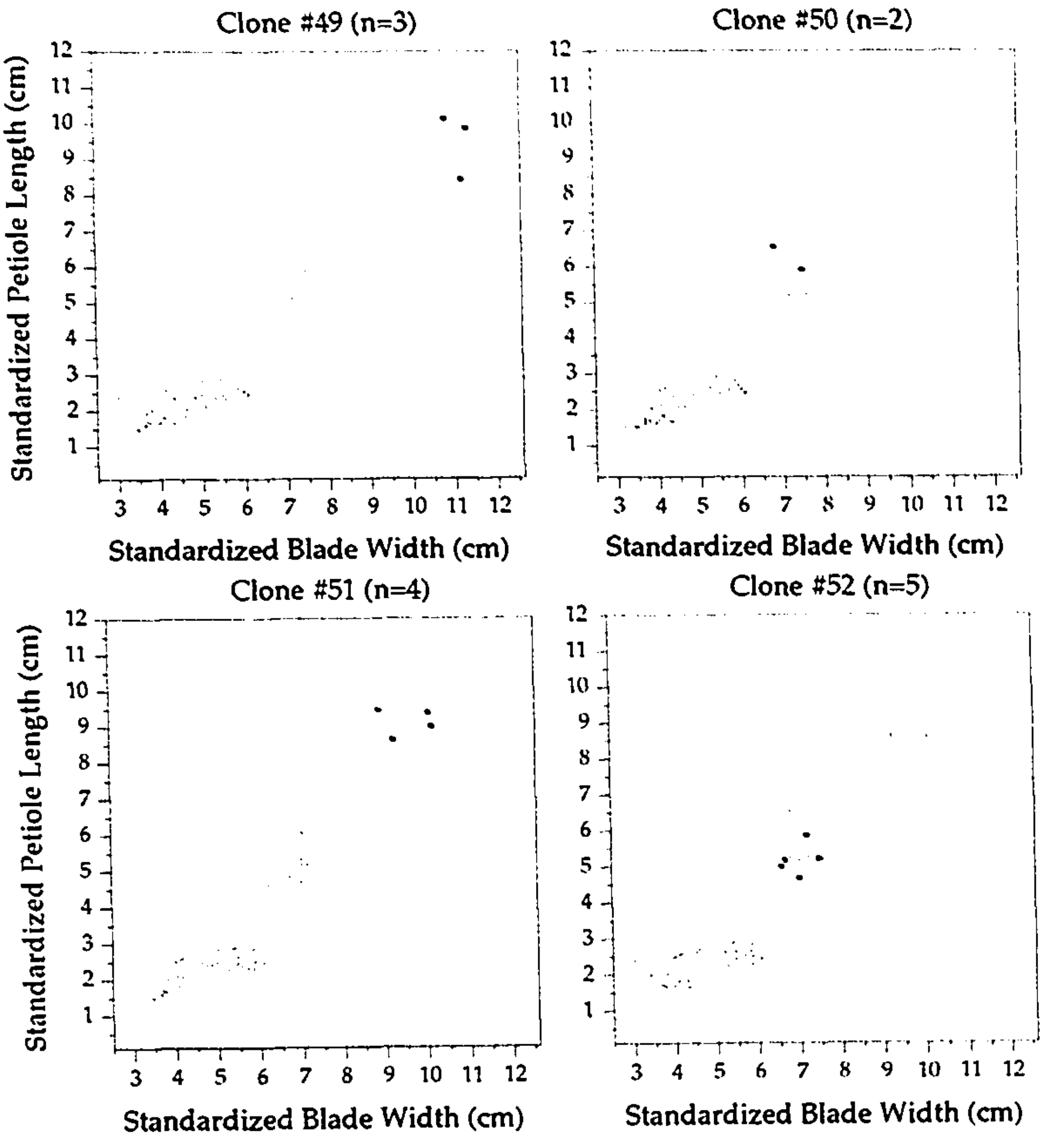
Clone #45 (n=3)

Clone #46 (n=4)

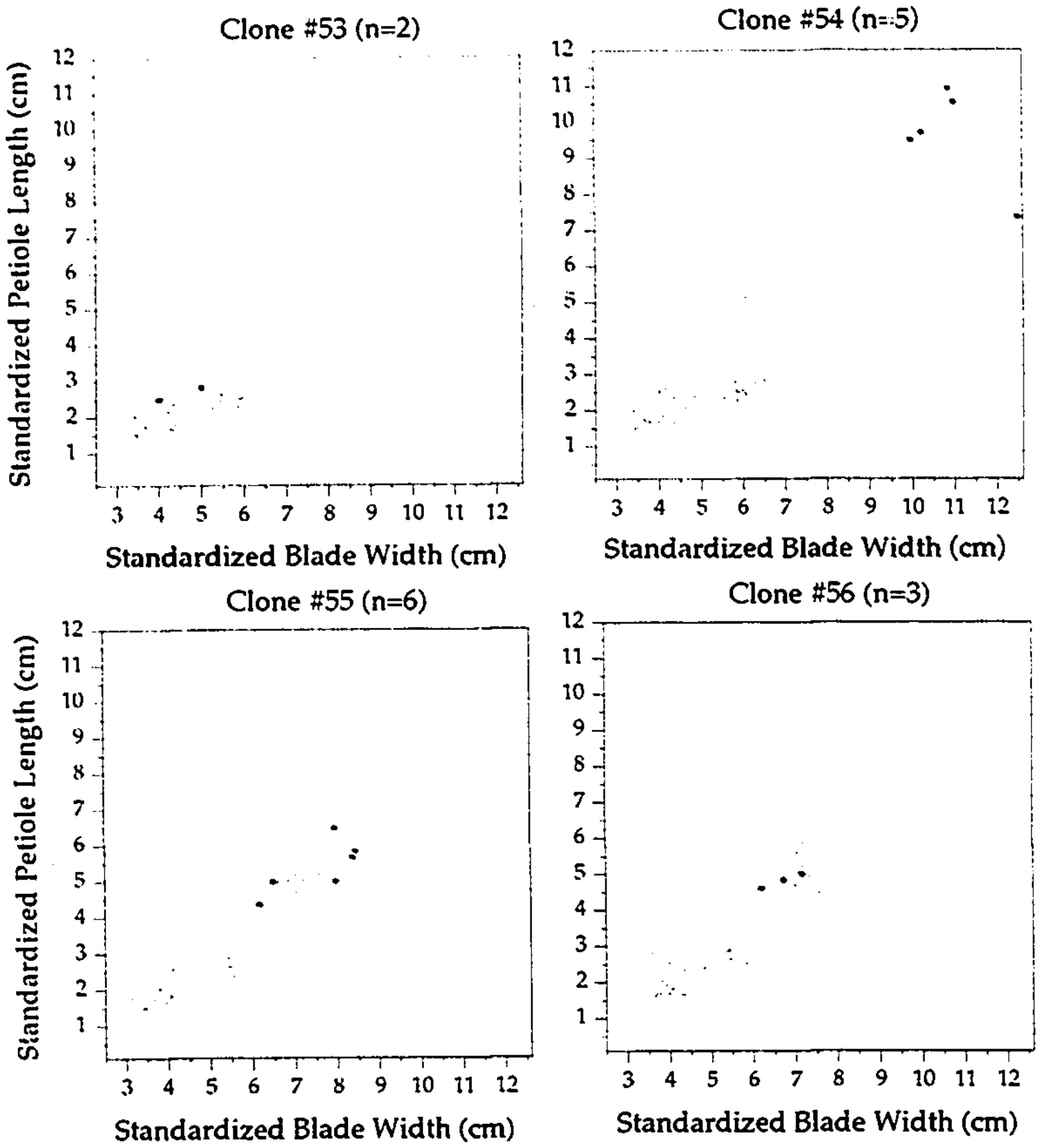
Clone #47 (n=4)

Clone #48 (n=3)

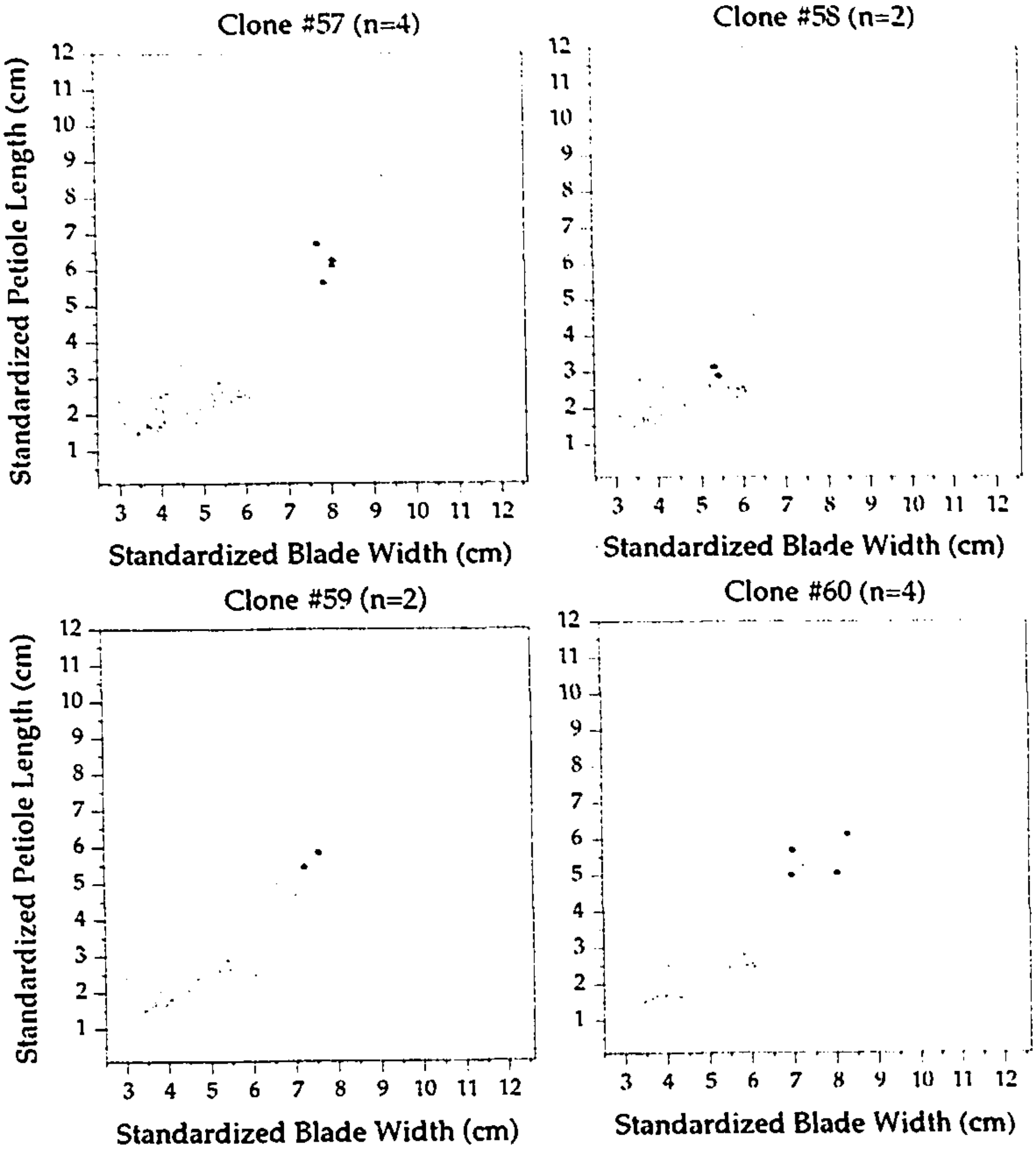
Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



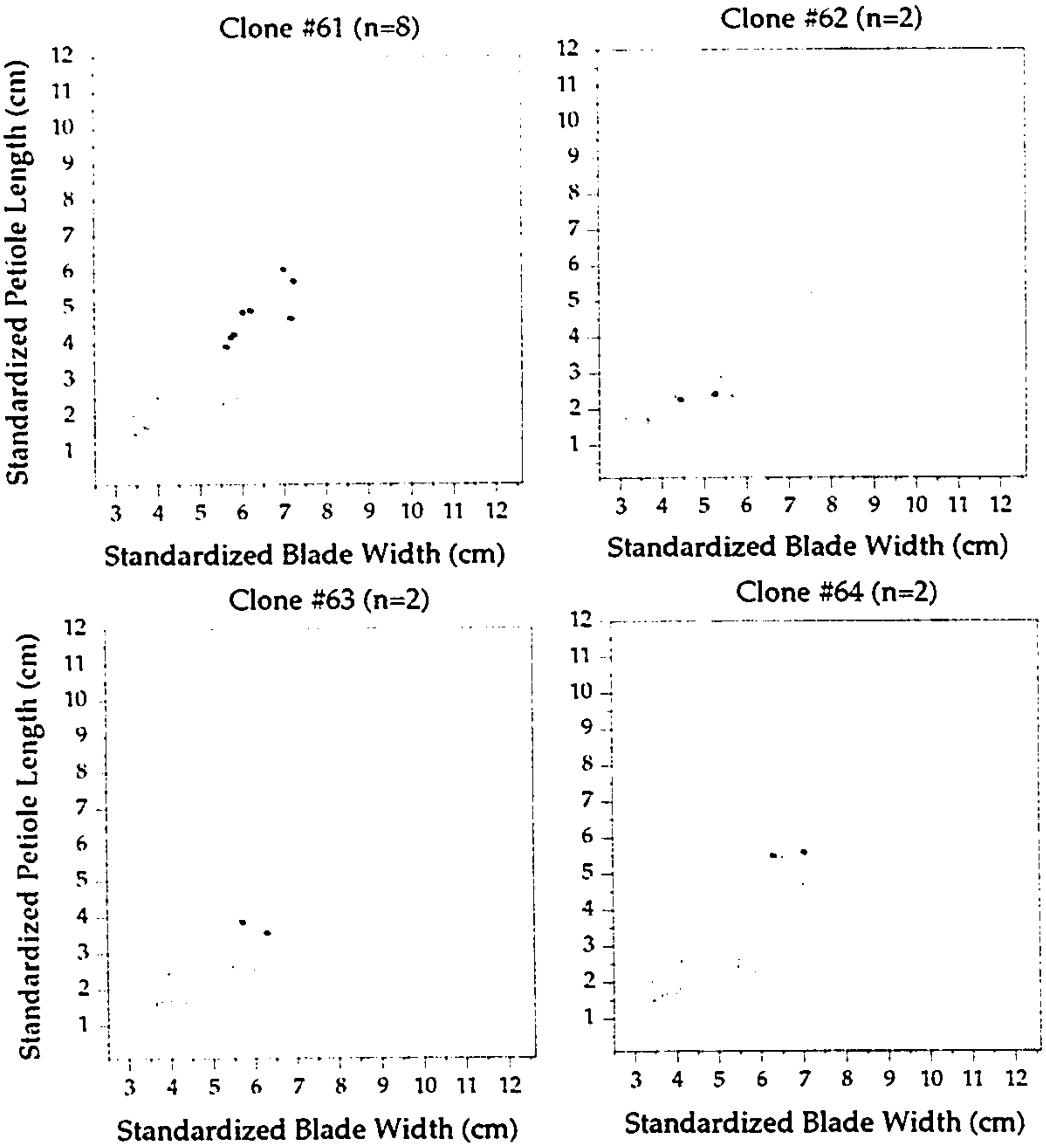
Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



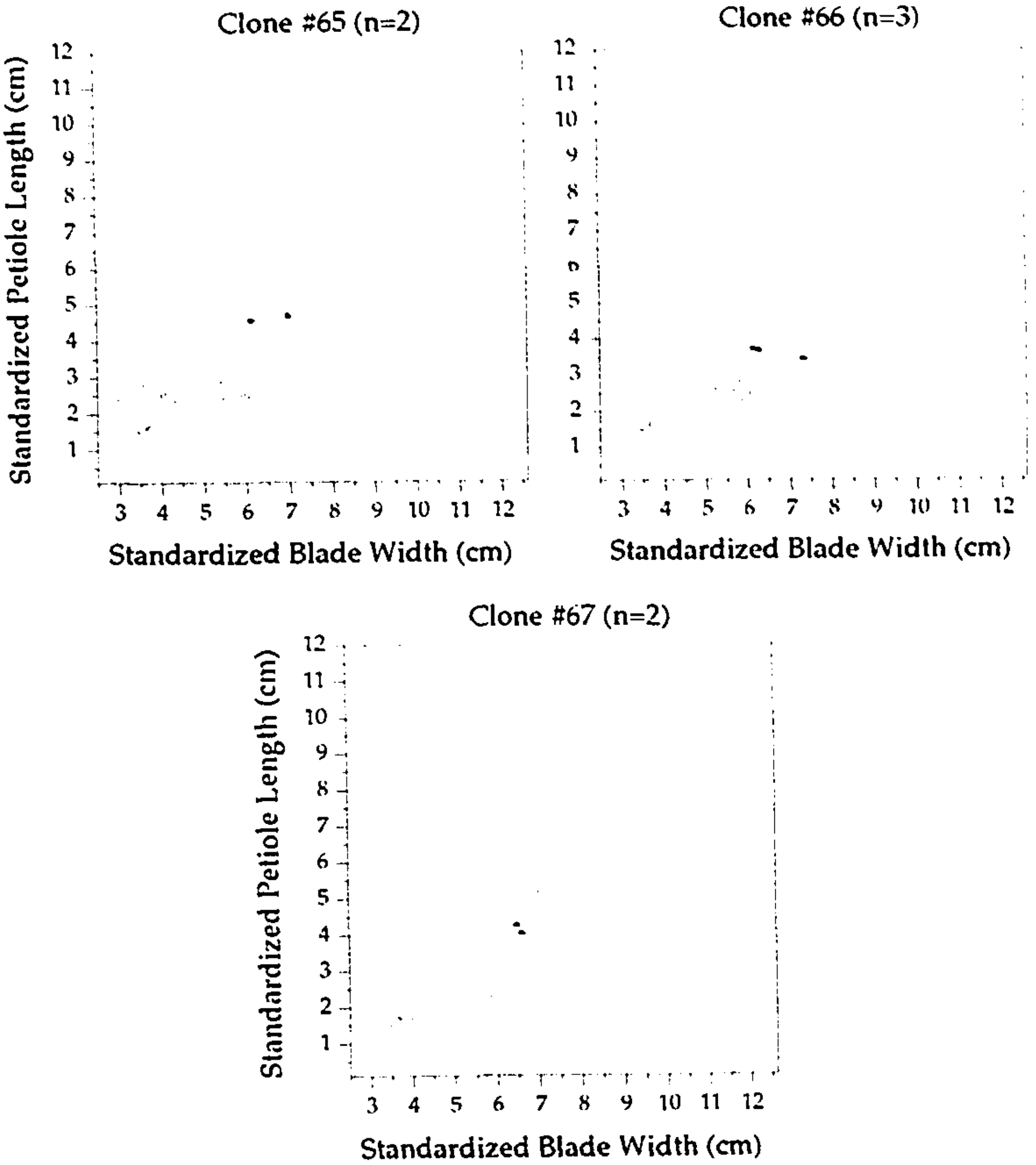
Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.



Continued - Figure 4-42. Summary of within-clone leaf measurement similarities (black) as compared with measurements from all trees on site.

4.3.2 Addressing the hypotheses:

Refer to section 2.0 (page 26), for explanations of the hypotheses. The first direction of inquiry sought evidence of asexual recruitment in the study population. The strongly clustered spatial distribution of characteristics could not be adequately explained by the proximal recruitment of siblings for several reasons. Firstly, the dispersal of pollen and seed in cottonwoods is wind-mediated and so should produce a mixed assortment and dispersal of seedlings. Secondly, the wide variability in leaf dimensions discovered among half-siblings suggests that, even if siblings established in close proximity, their phenotypes could still be distinguished. Thirdly, assuming an even sex ratio and non-clustered dispersal in cottonwood seeds, the observed clusters of same-sexed trees would rarely occur. Since the clusters of trees with shared heritable characteristics cannot be adequately explained by environment-directed selection or sibling-relatedness, there does appear to be evidence of asexual recruitment in the study population.

The second direction of inquiry asked if groupings of clonally-related mature cottonwoods could be hypothesized based on phenotype and spatial positioning. The phenotypic characters were ranked in order of utility according to their heritability and individual variability. Each characteristic was applied in turn to successively divide the population based on dissimilarity. After a final evaluation of relative proximity, it was possible to delineate spatially grouped individuals with shared heritable traits. These groups are now presented as putative clones.

The final direction of inquiry asked for a summary of the abundance of mature, clonally-related cottonwoods within the site, trends related to their characteristics, and implications for cottonwood regeneration in general. The following sections will communicate these findings.

4.3.3 Description of putative clones & implications to population structure:

The analysis of the 391 mature cottonwoods within the study population identified 67 putative clones and 48 single-trunked individuals. The sex, species, number of ramets, and distances between the ramets of each clone are summarized in Table 4-26. Table 4-25 outlines these characteristics for the single-trunked individuals. The spatial distributions of the clones according to sex and species are described in Fig. 4-43, and Fig. 4-44 respectively. Fig. 4-45 and Fig. 4-46 superimpose gall abundances and trunk circumferences at breast height over maps of clone distribution. It is immediately obvious that the clonal nature of this population has an extensive influence over the nature and spatial distribution of phenotypic characteristics. It is also appears that different types of trees exhibit differing patterns in clonality.

Some general trends in clonality were detected among the sexes and species-types (Table 4-27). Despite the highest average numbers of ramets per clone being found in female and section *Tacamahaca* clones, testing revealed insignificant differences between the sexes (Table 4-28), and between the three species-type categories (Table 4-29). However, the ratio of clonal trunks to single ones was significantly higher in the female sex (Table 4-30), and in the section *Tacamahaca* (Table 4-31). Since the three, large, female clones; #3, #6, and #2, are all female and also belong to the *Tacamahaca* species category, it is suspected that they strongly influenced these results.

An indication of clonality less prone to influence by disproportionately large numbers of ramets, compares the number of genets represented by multiple trunks (clonal-genets) to those by single trunks. Although there are proportionally more female clonal-genets than male ones (Table 4-27), the difference was not significant (Table 4-32). The larger proportion of clonal-

Table 4-26. Summary of sex, species-type, and the distances separating ramets, for each hypothesized clone.

Clone ID#:	# of ramets:	Average Dist. (m):	Standard deviation:	Minimum Dist. (m):	Maximum Dist. (m):	Clone Sex	Ave. Species-Type Code
1	6	7.49	4.98	0.64	16.79	M	2.5
2	11	8.45	6.03	0.64	20.43	F	3.0
3	53	20.68	11.06	0.25	51.65	F	3.5
4	6	2.53	1.81	0.71	5.99	M	3.0
5	3	1.46	0.62	0.98	2.16	F	5.0
6	20	15.23	8.55	0.59	31.95	F	2.5
7	4	1.02	0.37	0.56	1.42	F	2.0
8	3	0.71	0.27	0.45	0.99	F	1.0
9	3	7.70	6.03	0.75	11.52	M	2.0
10	7	2.94	2.64	0.51	7.97	F	1.5
11	3	0.80	0.24	0.54	1.01	F	2.5
12	3	1.97	1.10	0.77	2.92	M	8.0
13	4	2.22	1.29	0.92	3.72	F	4.0
14	2	0.50	—	0.50	0.50	F	3.0
15	8	11.12	6.54	0.64	25.13	F	2.0
16	11	5.14	2.90	0.55	10.68	M	1.5
17	3	2.52	1.59	0.71	3.70	F	2.5
18	3	0.79	0.15	0.63	0.92	F	3.0
19	18	12.40	6.52	0.52	31.01	F	5.0
20	6	2.82	1.40	0.47	4.99	M	6.0
21	5	5.75	2.86	0.59	8.85	M	2.0
22	2	0.67	—	0.67	0.67	F	8.0
23	3	0.76	0.30	0.56	1.10	F	8.0
24	2	1.17	—	1.17	1.17	M	2.0
25	2	0.74	—	0.74	0.74	F	5.0
26	5	3.01	1.21	1.72	5.55	M	2.5
27	8	2.34	1.22	0.59	5.03	F	5.0
28	3	1.23	0.25	1.04	1.51	M	5.5
29	7	3.10	1.56	0.74	5.64	F	5.0
30	2	1.08	—	1.08	1.08	F	8.0
31	6	2.66	1.49	0.77	4.67	F	5.0
32	2	1.05	—	1.05	1.05	F	8.0
33	4	5.91	4.30	1.04	10.65	M	2.5
34	2	2.04	—	2.04	2.04	F	8.0
35	5	1.93	0.79	0.62	3.10	M	5.0
36	4	3.85	2.86	0.65	7.15	M	5.0
37	2	0.73	—	0.73	0.73	M	5.0
38	2	0.83	—	0.83	0.83	F	7.5
39	2	1.35	—	1.35	1.35	F	8.0
40	2	1.25	—	1.25	1.25	M	8.0
41	9	6.62	3.85	0.55	14.15	M	3.0
42	2	9.42	—	9.42	9.42	M	2.0
43	5	2.87	2.58	0.63	6.35	F	2.0
44	3	3.20	1.75	1.28	4.70	M	2.0
45	3	2.62	1.28	1.15	3.51	F	3.5
46	4	8.61	5.78	0.61	13.42	M	5.0
47	4	1.89	0.97	0.70	3.10	?	5.0
48	3	5.66	4.35	0.64	8.48	M	8.0
49	3	8.72	6.56	1.18	13.07	M	8.0
50	2	0.54	—	0.54	0.54	F	5.0
51	4	7.85	5.43	0.58	15.43	F	7.0
52	5	6.03	3.22	2.00	12.67	F	5.0
53	2	5.77	—	5.77	5.77	M	2.0
54	5	21.56	13.36	0.71	45.84	F	8.0
55	6	10.34	6.53	0.99	20.00	F	5.0
56	3	4.17	1.33	3.06	5.65	?	5.0
57	4	1.00	0.34	0.64	1.56	M	5.5
58	2	0.65	—	0.65	0.65	M	3.5
59	2	0.77	—	0.77	0.77	M	5.5
60	4	1.84	0.73	0.77	2.43	F	5.0
61	8	5.90	3.61	0.69	11.33	F	5.0
62	2	0.81	—	0.81	0.81	?	3.0
63	2	1.17	—	1.17	1.17	?	3.0
64	2	1.00	—	1.00	1.00	F	5.0
65	2	1.12	—	1.12	1.12	M	5.0
66	3	0.98	0.28	0.75	1.29	M	5.0
67	2	1.48	—	1.48	1.48	?	5.0

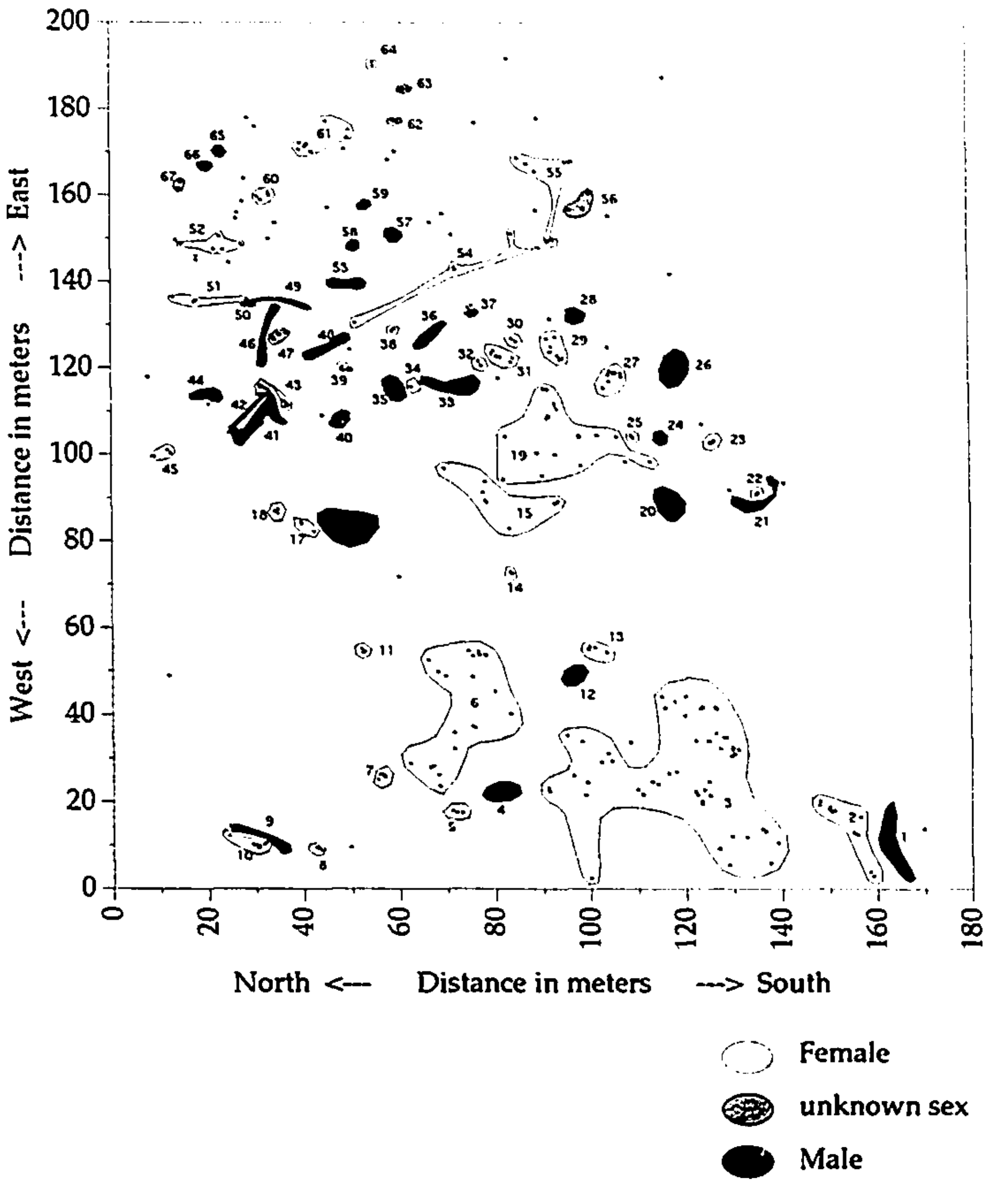


Figure 4-43. The spatial distribution of putative clones classified by sex. The labels indicate each clone's identification number.

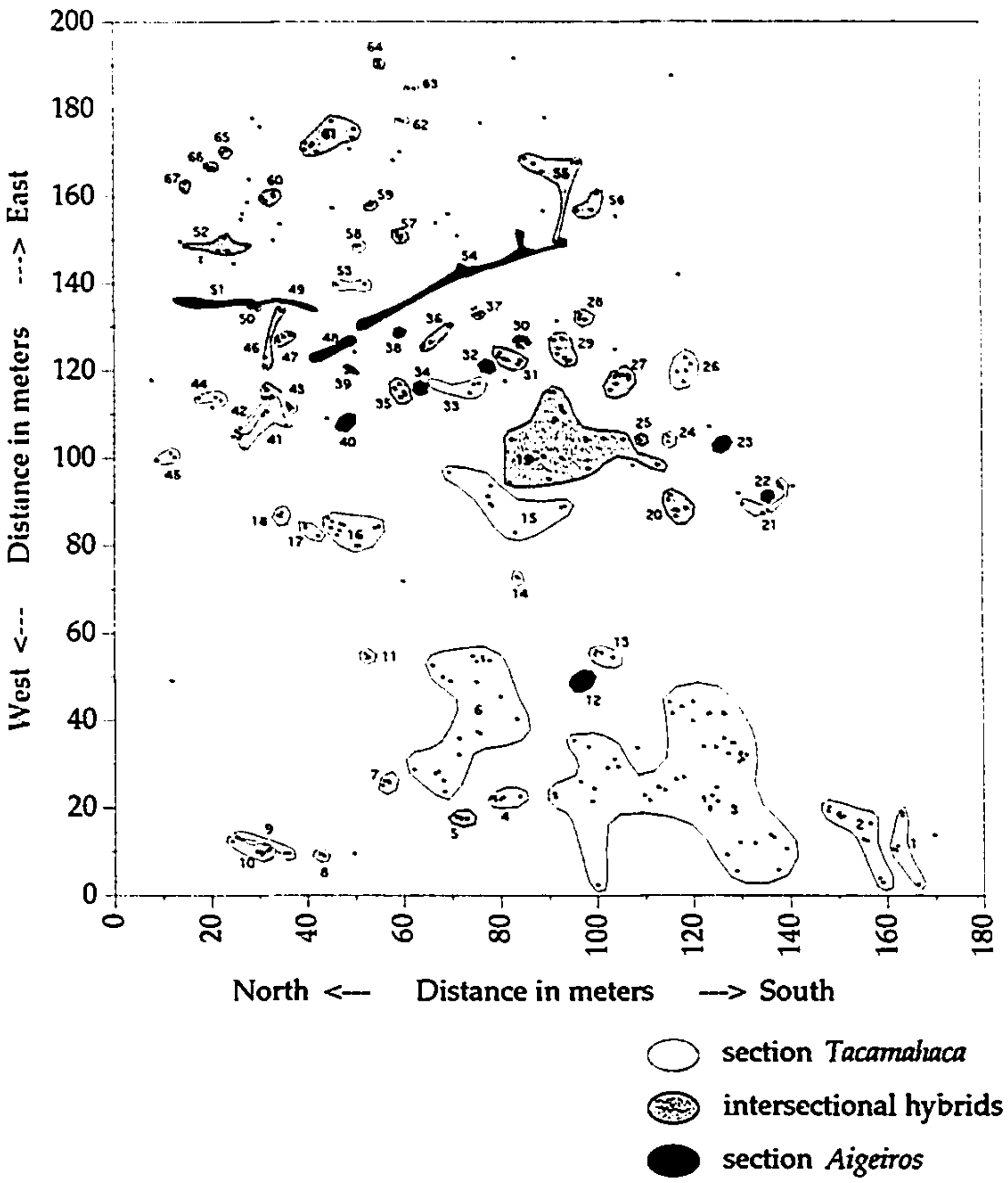


Figure 4-44. The spatial distribution of putative clones classified by species-type. The labels indicate each clone's identification number.

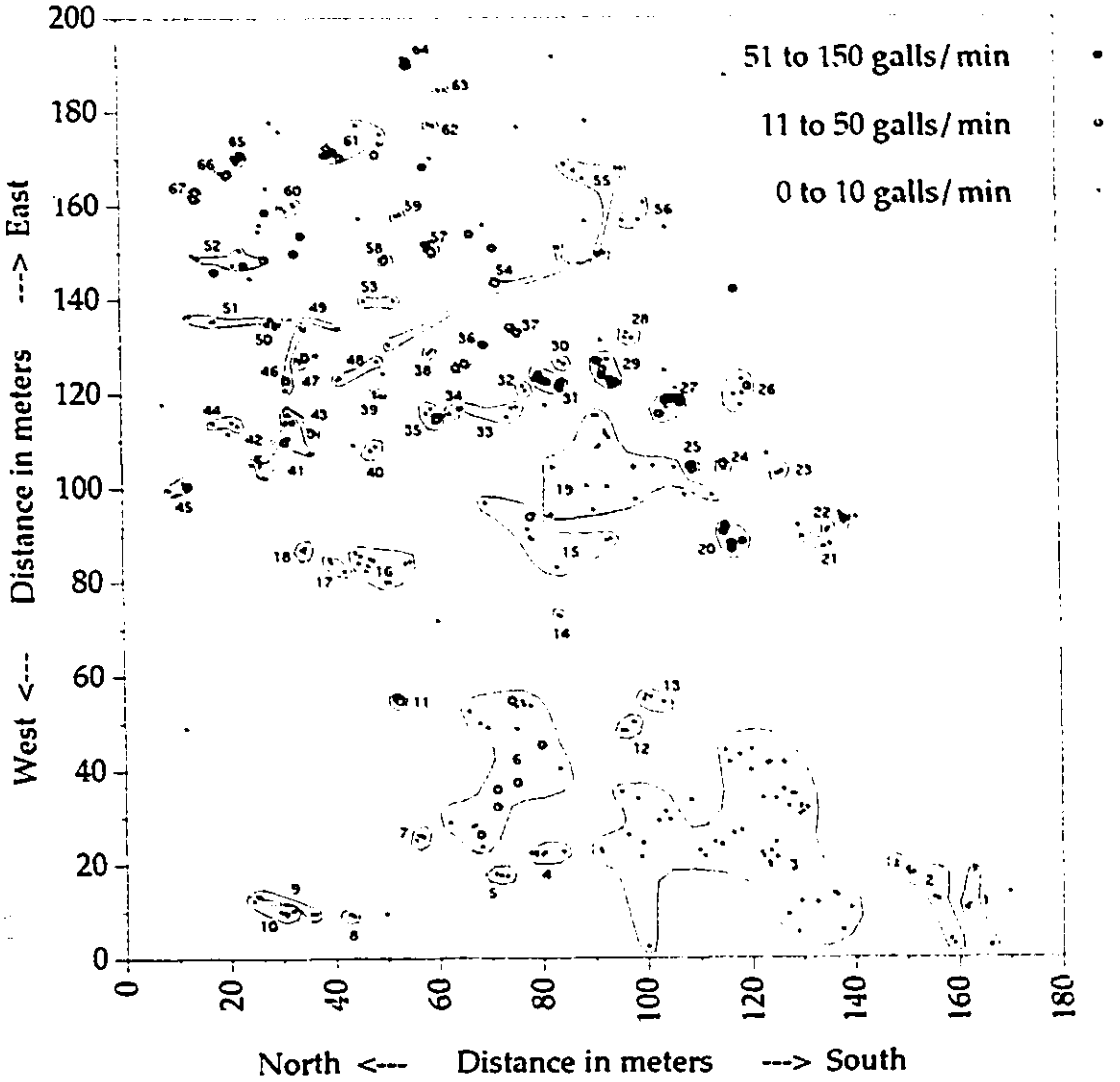


Figure 4-45. The spatial distribution of putative clones (labelled with their clone numbers), and the abundance of mite-galls for each trunk.

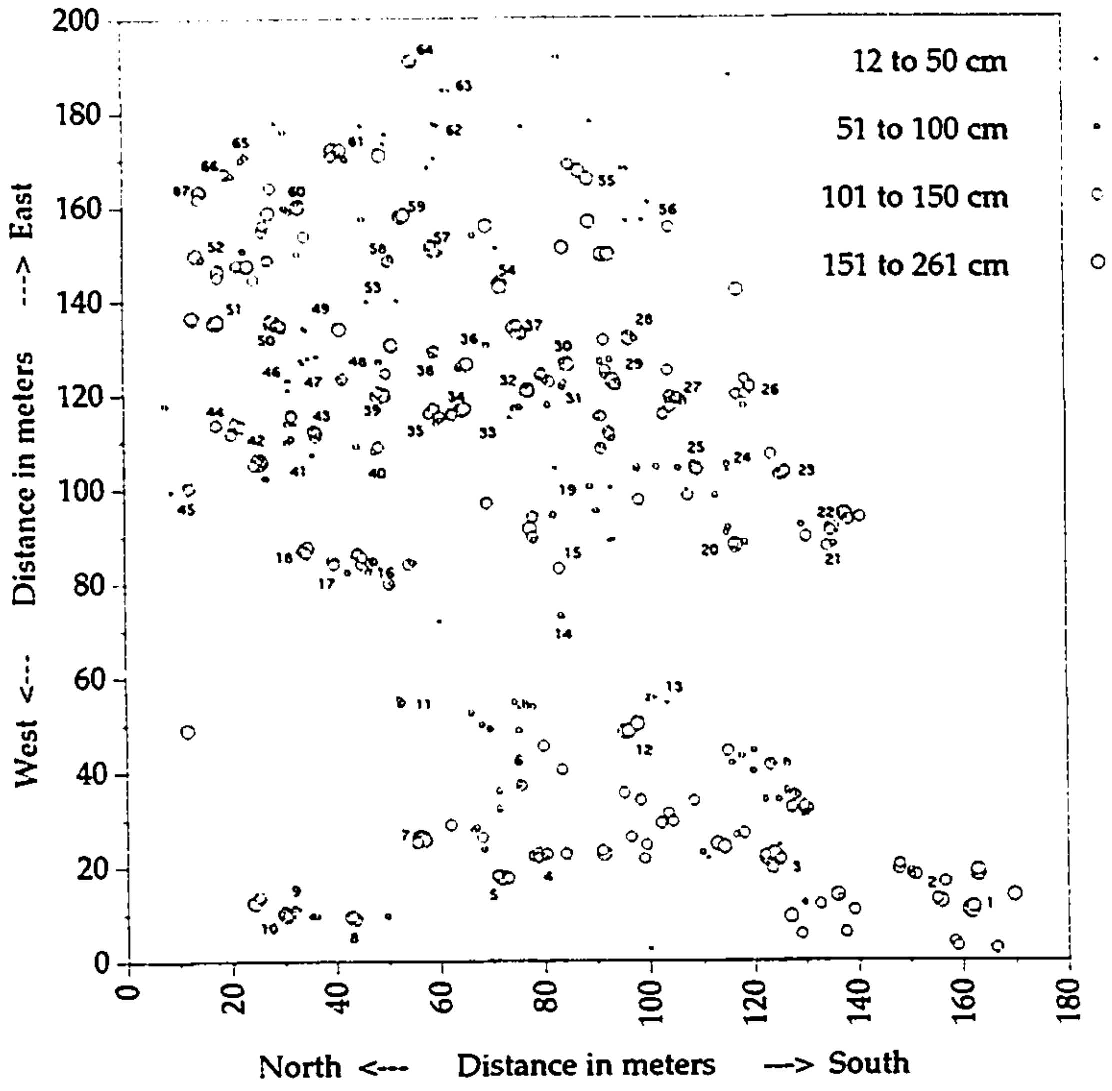


Figure 4-46. The spatial distribution of trunks within the putative clones. Four categories of trunk circumference at breast height are indicated by increasing symbol sizes, and clone numbers are also included).

Table 4-27. Summary of clones, ramets, and single trunks according to sex and species-type for the entire population (N=391).

		Number of Clones	Number of Ramets	Average number of Ramets per Clone	Number of Single Trunks	proportion of trunks belonging to clone groups (%)	proportion (%) of genets with multiple trunks
	Whole Site:	67	343	5.12	48	87.72	58.26
	All Females:	35	224	6.40	14	94.12	71.43
	All Males:	27	106	3.93	24	81.54	52.94
	All Unknowns:	5	13	2.60	10	56.52	33.33
Section Tacamahaca	(leaf-codes 1 to 4:)	29	193	6.66	18	91.47	61.70
	Females:	14	129	9.21	9	93.48	60.87
	Males:	13	60	4.62	4	93.75	76.47
	Unknowns:	2	4	2.00	5	44.44	28.57
intersectional hybrids	(leaf-codes 5 to 6.5:)	25	115	4.60	19	85.82	56.82
	Females:	12	71	5.92	1	98.61	92.31
	Males:	10	35	3.50	13	72.92	43.48
	Unknowns:	3	9	3.00	5	64.29	37.50
Section Aigeiros	(leaf-codes 7 to 8:)	13	35	2.69	11	76.09	54.17
	Females:	9	24	2.67	4	85.71	69.23
	Males:	4	11	2.75	7	61.11	36.36
	Unknowns:	0			0		

Table 4-28. Using the F-Test to determine whether the variance of number of ramets in male clones is significantly different from that in female clones, in order to choose the proper t-Test for testing whether the means of the two samples are significantly different.

F-Test: Two-Sample for Variances
Null Hypothesis: The two samples have the same variance.

	Male Clones	*Female Clones*
Mean	3.93	6.40
Variance	4.92	83.07
Observations	27	35
Degrees of Freedom	26	34
F	0.0592	
P (F<=f) one-tail	1.0000	
F Critical one-tail	0.5480	

Decision: Do not reject the Null Hypothesis
Conclusion: <u>The variances are not significantly different,</u> therefore use the following t-Test:

t-Test: Two-Sample Assuming Equal Variances
Null Hypothesis: The two samples have the same mean.
(the mean abundances of galls are not significantly different in males versus females)

Degrees of freedom	60
t Stat	-1.3770
P (T<=t) one-tail	0.0868
t Critical one-tail	1.6706
P (T<=t) two-tail	0.1736
t Critical two-tail	2.0003

Decision: Do not reject the Null Hypothesis
Conclusion: <u>The sample means do not differ significantly</u>
-the mean number of ramets in male vs. female clones is not significantly different

Table 4-29. Using an ANOVA to detect differences between the mean number of ramets in clones belonging to section *Tacamahaca,* section *Aigeiros,* and intersectional hybrids.

SUMMARY:

Categories:	*Count*	*Sum*	*Average*	*Variance*
A to B (*Tacamahaca*)	29	193	6.66	94.52
AD to BD (intersectional)	25	115	4.60	11.42
DB to D (*Aigeiros*)	13	35	2.69	0.90

ANOVA: Single Factor

Null Hypothesis: The three categories have the same mean number of ramets per clone.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between categories	151.72	2	75.86	1.6563	0.1989	3.1404
Within categories	2931.32	64	45.80			
Total	3083.05	66				

Decision: Do not reject the Null Hypothesis

Conclusion: The mean number of ramets per clone in the three species-categories are not significantly different.

Table 4-30. Using the X^2 Test of Independence: Do males and females differ in their ratios of clonal to single trunks?

(Contingency Table:)

		Number of trunks occurring as:		
		Ramets of clones:	Single trunks:	Totals:
Females:	Obs:	224	14	238
	Exp:	213.42	24.58	238
Males:	Obs:	106	24	130
	Exp:	116.58	13.42	130
Column Totals:		330	38	368

Null Hypothesis: The ratio of trunks occurring as ramets to those occurring singly, is the same in males as in females.

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 14.3673$

$df = 1 \therefore$ critical X^2 value $= 3.84$ $(\alpha=0.05)$

Since $14.3673 > 3.84 \therefore$ Reject the Null Hypothesis

Conclusion: Males and females do differ significantly in their ratios of trunks occurring as ramets to those occurring singly; females have a significantly higher ratio of ramets to single trunks than males do.

Table 4-31. Using the X^2 Test of Independence: To determine whether the ratio of the number of trunks belonging to clones and the number of trunks occurring singly, differs significantly among the three species-categories.

(Contingency Table:)

		Number of trunks occurring as:		
		Ramets:	Single trunks:	Totals:
Section *Tacamahaca*:	Obs:	193	18	211
	Exp:	185.10	25.90	211
Intersectional Hybrids:	Obs:	115	19	134
	Exp:	117.55	16.45	134
Section *Aigeiros*:	Obs:	35	11	46
	Exp:	40.35	5.65	46
Column Totals:		343	48	391

Null Hypothesis: Members of the three species-related categories have the same occurrence of branch sacrifice.

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 8.9833$

df = 2 $\therefore$ critical X^2 value = 5.99 (α=0.05)

Since $8.9833 > 5.99$ $\therefore$ Reject the Null Hypothesis

Conclusion: The ratio of ramets to single trunks does differ significantly among the three species-categories;
Section *Tacamahaca* had the highest proportion of ramets to single trunks, the intersectional hybrids were intermediate, and section *Aigeiros* had the lowest proportion.

genets in the *Tacamahaca* section was likewise not significant (Table 4-33). Since the number of ramets per clone and the ratio of clonal versus non-clonal genets do not vary significantly between the sexes or species, the population has been found to be fairly homogeneous for these clonal characteristics. For this reason, the population-based trends can be used to summarize the tendencies of the whole population. The average number of ramets per clone was thus 5.12, and the proportion of multiple-trunked genets was 58.26%. The three large, female clones belonging to section *Tacamahaca* suggest that cottonwoods of this type produce larger numbers of ramets. However, this observation needs substantiation based on surveys of larger numbers of genets before findings can be conclusive.

Inter-ramet distances are listed in Table 4-26, and their averages are summarized according to sex and species-type in Table 4-34. When the average, minimum, and maximum distances between the ramets of each clone were tested for differences between the sexes and species categories, no significant differences were detected (Table 4-35, Table 4-36, Table 4-37, Table 4-38, Table 4-39, and Table 4-40). Since significant differences were not detected among the sexes or species, the trends in inter-ramet distances for the population can be summarized by an average ramet spacing of 4.07 m and an average clone diameter of 7.54 m.

The close spacing of adjacent ramets appears to show variable occurrence among clones (Table 4-41). However, testing concluded that these differences between male and female clones, and between clones of section *Tacamahaca*, section *Aigciros*, or intersectional hybrids, were not significant (Table 4-42 and Table 4-43).

Table 4-32. Using the X^2 Test of Independence: Do males and females differ in their ratios of multiple-trunked individuals to single-trunked individuals?

(Contingency Table:)

		Number of Genets represented by: multiple trunks:	one trunk:	Totals:
Females:	Obs:	35	14	49
	Exp:	30.38	18.62	49
Males:	Obs:	27	24	51
	Exp:	31.62	19.38	51
Column Totals:		62	38	100

Null Hypothesis: The ratio of multiple to single-trunked individuals is the same in males as in females.

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 3.6253$

df = 1 $\therefore$ critical X^2 value = 3.84 (α=0.05)

Since $3.6253 < 3.84$ $\therefore$ fail to reject the Null Hypothesis

Conclusion: The ratio of multiple to single-trunked individuals is not significantly different between males and females.

Table 4-33. Using the X^2 Test of Independence: To determine whether the ratio of multiple-trunked genets to single-trunked ones differs significantly among the three species-categories.

(Contingency Table:)

		Number of genets represented by: multiple trunks:	one trunk:	Totals:
Section *Tacamahaca:*	Obs:	29	18	47
	Exp:	27.38	19.62	47
Intersectional Hybrids:	Obs:	25	19	44
	Exp:	25.63	18.37	44
Section *Aigeiros:*	Obs:	13	11	24
	Exp:	13.98	10.02	24
Column Totals:		67	48	115

Null Hypothesis: The ratio of multiple-trunked individuals/genets to single-trunked ones is the same among all three species-categories.

$X^2 = \sum \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 0.4320$

$\text{df} = 2 \therefore$ critical X^2 value $= 5.99$ $(\alpha=0.05)$

Since $0.4320 < 5.99$ $\therefore$ do not reject the Null Hypothesis

Conclusion: The ratio of multiple-trunked genets to single-trunked ones is not significantly different between the three species-categories.

Table 4-34. Average of the average, minimum, and maximum inter-ramet distances for all clones according to their sex and species-categories.

		Ramet Spacing	Closest Ramet Proximity	Clone Size (Diameter)
		Ave. of Ave. inter-ramet distance (m)	Ave. minimum inter-ramet distance (m)	Ave. maximum inter-ramet distance (m)
	Whole Site:	4.07	1.06	7.54
	All Females:	4.51	0.80	9.31
	All Males:	3.89	1.34	6.19
	All Unknowns:	1.90	1.44	2.44
Section Tacamahaca	(leaf-code 1 to 4:)	4.79	1.23	9.21
	Females:	5.18	0.62	11.37
	Males:	4.95	1.91	8.15
	Unknowns:	0.99	0.99	0.99
intersectional hybrids	(leaf-code 5 to 6.5:)	3.16	0.92	5.72
	Females:	4.03	0.86	8.10
	Males:	2.30	0.74	3.56
	Unknowns:	2.51	1.75	3.41
Section Aigeiros	(leaf-code 7 to 8:)	4.21	0.98	7.32
	Females:	4.13	0.99	7.71
	Males:	4.40	0.96	6.43
	Unknowns:	N/A	N/A	N/A

Table 4-35. Using the F-Test to determine whether the variance among the average distances separating the ramets of male clones is significantly different from that found in female clones, in order to choose the proper t-Test for testing whether the means of the two samples are significantly different.

F-Test: Two-Sample for Variances
Null Hypothesis: The two samples have the same variance.

	Male Clones	*Female Clones*
Mean	3.89	4.51
Variance	8.27	31.67
Observations	27	35
Degrees of Freedom	26	34
F	0.2610	
P (F<=f) one-tail	0.9998	
F Critical one-tail	0.5480	

Decision: Do not reject the Null Hypothesis
Conclusion: The variances are not significantly different, therefore use the following t-Test:

t-Test: Two-Sample Assuming Equal Variances
Null Hypothesis: The two samples have the same mean.
(the mean average distances between ramets found in male versus female clones do not differ significantly)

Degrees of freedom	60
t Stat	-0.5259
P (T<=t) one-tail	0.3004
t Critical one-tail	1.6706
P (T<=t) two-tail	0.6009
t Critical two-tail	2.0003

Decision: Do not reject the Null Hypothesis
Conclusion: The sample means do not differ significantly

Table 4-36. Using the F-Test to determine whether the variance among the minimum distances separating the ramets of male clones is significantly different from that found in female clones, in order to choose the proper t-Test for testing whether the means of the two samples are significantly different.

F-Test: Two-Sample for Variances
Null Hypothesis: The two samples have the same variance.

	Male Clones	*Female Clones*
Mean	1.34	0.80
Variance	3.60	0.14
Observations	27	35
Degrees of Freedom	26	34
F	25.0662	
P (F<=f) one-tail	1.93E-15	
F Critical one-tail	1.8248	

Decision: Reject the Null Hypothesis
Conclusion: The variances are significantly different, therefore use the following t-Test:

t-Test: Two-Sample Assuming Unequal Variances
Null Hypothesis: The two samples have the same mean.
(the mean minimum distances between ramets found in male vs. female clones do not differ significantly)

Degrees of freedom	28
t Stat	1.4528
P (T<=t) one-tail	0.0787
t Critical one-tail	1.7011
P (T<=t) two-tail	0.1574
t Critical two-tail	2.0484

Decision: Do not reject the Null Hypothesis
Conclusion: The sample means do not differ significantly

Table 4-37. Using the F-Test to determine whether the variance among the maximum distances separating the ramets of male clones is significantly different from that found in female clones, in order to choose the proper t-Test for testing whether the means of the two samples are significantly different.

F-Test: Two-Sample for Variances
Null Hypothesis: The two samples have the same variance.

	Male Clones	*Female Clones*
Mean	6.19	9.31
Variance	24.03	174.83
Observations	27	35
Degrees of Freedom	26	34
F	0.1374	
P (F<=f) one-tail	1.0000	
F Critical one-tail	0.5480	

Decision: Do not reject the Null Hypothesis
Conclusion: The variances are not significantly different, therefore use the following t-Test:

t-Test: Two-Sample Assuming Equal Variances
Null Hypothesis: The two samples have the same mean.
(the mean maximum distances between ramets found in male vs. female clones do not differ significantly)

Degrees of freedom	60
t Stat	-1.1625
P (T<=t) one-tail	0.1248
t Critical one-tail	1.6706
P (T<=t) two-tail	0.2496
t Critical two-tail	2.0003

Decision: Do not reject the Null Hypothesis
Conclusion: The sample means do not differ significantly

Table 4-38. Using an ANOVA to detect differences between the means of the average distances separating the ramets of clones belonging to section *Tacamahaca*, section *Aigeiros*, and intersectional hybrids.

SUMMARY:

Categories:	*Count*	*Sum*	*Average*	*Variance*
A to B (*Tacamahaca*)	29	138.81	4.79	22.62
AD to BD (intersectional)	25	78.91	3.16	10.07
DB to D (*Aigeiros*)	13	54.79	4.21	34.90

ANOVA: Single Factor

Null Hypothesis: The three categories have the same mean average distance between the ramets of each clone.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between categories	36.02	2	18.01	0.8908	0.4154	3.1404
Within categories	1293.99	64	20.22			
Total	1330.01	66				

Decision: Do not reject the Null Hypothesis

Conclusion: The mean average distances separating the ramets of clones in the three species-categories are not significantly different.

Table 4-39. Using an ANOVA to detect differences between the means of the minimum distances separating the ramets of clones belonging to section *Tacamahaca*, section *Aigeiros*, and intersectional hybrids.

SUMMARY:

Categories:	*Count*	*Sum*	*Average*	*Variance*
A to B (*Tacamahaca*)	29	35.54	1.23	3.44
AD to BD (intersectional)	25	22.97	0.92	0.31
DB to D (*Aigeiros*)	13	12.71	0.98	0.17

ANOVA: Single Factor

Null Hypothesis: The three categories have the same mean minimum distance between the ramets of each clone.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between categories	1.38	2	0.6893	0.4168	0.6609	3.1404
Within categories	105.85	64	1.6539			
Total	107.23	66				

Decision: Do not reject the Null Hypothesis

Conclusion: The mean minimum distances separating the ramets of clones in the three species-categories are not significantly different.

Table 4-40. Using an ANOVA to detect differences between the means of the maximum distances separating the ramets of clones belonging to section *Tacamahaca*, section *Aigeiros*, and intersectional hybrids.

SUMMARY:

Categories:	*Count*	*Sum*	*Average*	*Variance*
A to B (*Tacamahaca*)	29	267.12	9.21	127.19
AD to BD (intersectional)	25	143.07	5.72	51.70
DB to D (*Aigeiros*)	13	95.11	7.32	158.93

ANOVA: Single Factor

Null Hypothesis: The three categories have the same mean maximum distance between the ramets of each clone.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between categories	164.21	2	82.10	0.7832	0.4613	3.1404
Within categories	6709.19	64	104.83			
Total	6873.39	66				

Decision: Do not reject the Null Hypothesis

Conclusion: The mean maximum distances separating the ramets of clones in the three species-categories are not significantly different.

Table 4-41. Numbers of clones having one or more instance where two or more ramets were spaced less than 5 cm apart or were abutted at their bases. The instances are summarized according to the sex and species of the clones.

		Total Number of Clones	Number of clones having closely-spaced ramets	Number of clones not having closely-spaced ramets	Percent of clones having closely-spaced ramets
	Whole Site:	67	32	35	47.8
	All Females:	35	21	14	60.0
	All Males:	27	11	16	40.7
	Unknowns:	5	0	5	0.0
Section Tacamahaca	(Species 1 to 4:)	29	16	13	55.2
	Females:	14	11	3	78.6
	Males:	13	5	8	38.5
	Unknowns:	2	0	2	0.0
intersectional hybrids	(Species 5 to 6.5:)	25	10	15	40.0
	Females:	12	6	6	50.0
	Males:	10	4	6	40.0
	Unknowns:	3	0	3	0.0
Section Aigeiros	(Species 7 to 8:)	13	6	7	46.2
	Females:	9	4	5	44.4
	Males:	4	2	2	50.0
	Unknowns:	0	0	0	N/A

Tabie 4-42. Using the X^2 Test of Independence: To determine if the ratio of clones with closely-spaced ramets to those without, differs significantly between the sexes.

(Contingency Table:)

		Number of clones with closely-spaced ramets:	Number of clones without closely-spaced ramets:	Totals:
Females:	Obs:	21	14	35
	Exp:	18.06	16.94	35
Males:	Obs:	11	16	27
	Exp:	13.94	13.06	27
Column Totals:		32	30	62

Null Hypothesis: The ratio of clones with closely-spaced ramets to those without is the same in males as in females.

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 2.2638$

df = 1 $\therefore$ critical X^2 value = 3.84 (α=0.05)

Since $2.2638 < 3.84$ $\therefore$ fail to reject the Null Hypothesis

Conclusion: The ratio of clones with closely-spaced ramets to those without, does not differ significantly between males and females.

Table 4-43. Using the X^2 Test of Independence: To determine if the ratio of clones with closely-spaced ramets to clones without, differs significantly between the three species-categories.

(Contingency Table:)

		Number of clones <u>with</u> closely-spaced ramets:	Number of clones <u>without</u> closely-spaced ramets:	Totals:
<u>Section</u>	Obs:	16	13	29
<u>*Tacamahaca:*</u>	Exp:	13.85	15.15	29
<u>Intersectional</u>	Obs:	10	15	25
<u>Hybrids:</u>	Exp:	11.94	13.06	25
<u>Section</u>	Obs:	6	7	13
<u>*Aigeiros:*</u>	Exp:	6.21	6.79	13
Column Totals:		32	35	67

<u>Null Hypothesis:</u> The ratio of clones with closely-spaced ramets to those without, is the same in all three species-categories.

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 1.2555$

df = 2 $\therefore$ critical X^2 value = 5.99 (α=0.05)

Since $1.2555 < 5.99$ $\therefore$ do not reject the Null Hypothesis

<u>Conclusion:</u> The ratio of clones with closely-spaced ramets to those without, does not differ significantly between the three species-categories.

Since trunk circumference at breast height is a general index of tree size and thus maturity, the range in circumference among ramets of a clone reflects the range in ages of those trunks. The minimum, maximum, and average trunk circumferences found among the ramets of each clone are presented in Table 4-44. When the differences between the minimum and maximum values were analyzed for trends related to sex and species, none were found (Table 4-45 and Table 4-46). The population-based average difference between the two extremes of ramet circumference was 67.19 cm. This average difference represents approximately 26% of the circumference of the largest ramet on site. In order to have such a high degree of within-clone circumference variability, clonal sprouts must have been initiated throughout the lifetime of the clones. Clones with larger numbers of ramets tend to have a greater potential for spread among their ramets' circumferences (Fig. 4-47), and so appear to have been continually replenished over longer periods of time.

There are important implications when the clonal contribution to population structure is recognized. Since ramets represent genome duplications, those genotypic proportions can become amplified, causing a skewed population. The sex ratio of the study population exemplifies this effect. When initial observations identified the characteristics of each trunk separately, there was a strongly female-biased sex ratio. However, this skew can now be explained by a disproportionately high number of female ramets. Following clonal evaluation, the sex ratio of genets was found not to be biased towards either sex (Table 4-47 a). Even when genets of unknown sex are included as males, the sex ratio is considered to be about equal (Table 4-47 b).

Table 4-44. Summary of ramet trunk circumferences in each clone.

Clone I.D. #	Total # of Ramets	Sex of the Clone	Average Clone Species:	Minimum Ramet Circ (cm)	Maximum Ramet Circ (cm)	Average Ramet Circ (cm)
1	6	M	2.5	147	221	184.5
2	11	F	3.0	77	162	112.5
3	53	F	3.5	17	183	110.5
4	6	M	3.0	91	121	106.8
5	3	F	5.0	123	155	141.3
6	20	F	2.5	44	114	87.9
7	4	F	2.0	117	172	156.5
8	3	F	1.0	105	160	126.7
9	3	M	2.0	83	110	92.7
10	7	F	1.5	55	186	127.3
11	3	F	2.5	56	66	60.0
12	3	M	8.0	209	238	228.3
13	4	F	4.0	28	42	33.3
14	2	F	3.0	50	67	58.5
15	8	F	2.0	23	160	89.3
16	11	M	1.5	57	139	95.8
17	3	F	2.5	97	127	114.3
18	3	F	3.0	125	153	140.3
19	18	F	5.0	20	125	84.0
20	6	M	6.0	73	184	110.7
21	5	M	2.0	60	206	137.0
22	2	F	8.0	140	152	146.0
23	3	F	8.0	126	138	131.7
24	2	M	2.0	45	97	71.0
25	2	F	5.0	102	150	126.0
26	5	M	2.5	99	145	120.0
27	8	F	5.0	80	127	104.3
28	3	M	5.5	67	200	120.3
29	7	F	5.0	57	166	96.1
30	2	F	8.0	85	169	127.0
31	6	F	5.0	30	124	85.7
32	2	F	8.0	95	172	133.5
33	4	M	2.5	34	163	82.5
34	2	F	8.0	127	156	141.5
35	5	M	5.0	87	129	105.4
36	4	M	5.0	53	234	116.8
37	2	M	5.0	109	165	137.0
38	2	F	7.5	51	131	91.0
39	2	F	8.0	148	166	157.0
40	2	M	8.0	98	130	114.0
41	9	M	3.0	25	169	93.8
42	2	M	2.0	47	88	67.5
43	5	F	2.0	66	130	98.4
44	3	M	2.0	106	147	127.7
45	3	F	3.5	15	143	68.7
46	4	M	5.0	22	35	28.0
47	4	?	5.0	21	29	25.5
48	3	M	8.0	73	139	101.7
49	3	M	8.0	148	190	171.7
50	2	F	5.0	142	189	165.5
51	4	F	7.0	178	232	202.5
52	5	F	5.0	54	164	107.6
53	2	M	2.0	21	29	25.0
54	5	F	8.0	172	261	202.0
55	6	F	5.0	17	185	120.8
56	3	?	5.0	18	25	20.7
57	4	M	5.5	107	172	140.0
58	2	M	3.5	70	103	86.5
59	2	M	5.5	156	186	171.0
60	4	F	5.0	86	165	110.3
61	8	F	5.0	39	243	109.4
62	2	?	3.0	26	37	31.5
63	2	?	3.0	25	49	36.5
64	2	F	5.0	47	163	105.0
65	2	M	5.0	72	93	82.5
66	3	M	5.0	29	143	75.0
67	2	?	5.0	132	192	162.0

Table 4-45. Using the F-Test to determine whether the variance in the difference between the maximum and minimum circumferences of ramets in female versus male clones is significantly different, in order to choose the proper t-Test for testing whether the means of the two samples are significantly different.

F-Test: Two-Sample for Variances
Null Hypothesis: The two samples have the same variance.

	Female Clones	*Male Clones*
Mean	74.40	66.22
Variance	2455.07	2224.56
Observations	35	27
Degrees of Freedom	34	26
F	1.1036	
P (F<=f) one-tail	0.4020	
F Critical one-tail	1.8789	

Decision: Do not reject the Null Hypothesis
Conclusion: The variances are not significantly different, therefore use the following t-Test:

t-Test: Two-Sample Assuming Equal Variances
Null Hypothesis: The two samples have the same mean.

Degrees of freedom	60
t Stat	0.6579
P (T<=t) one-tail	0.2566
t Critical one-tail	1.6706
P (T<=t) two-tail	0.5131
t Critical two-tail	2.0003

Decision: Do not reject the Null Hypothesis
Conclusion: The sample means do not differ significantly

Table 4-46. Using an ANOVA to detect variance between the means of the differences between the largest and smallest trunk circumferences per clone, from the three species-categories.

SUMMARY:

Categories:	*Count*	*Sum*	*Average*	*Variance*
A to B (*Tacamahaca*)	29	1878	64.76	2333.83
AD to BD (intersectional)	25	2000	80.00	2968.33
DB to D (*Aigeiros*)	13	624	48.00	809.00

ANOVA: Single Factor

Null Hypothesis: The three species-categories have the same mean differences between the maximum and minimum circumferences per clone.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between categories	9061.17	2	4530.58	1.9820	0.1462	3.1404
Within categories	146295.31	64	2285.86			
Total	155356.478	66				

Decision: Do not reject the Null Hypothesis

Conclusion: The mean does not differ significantly between the three species-categories.

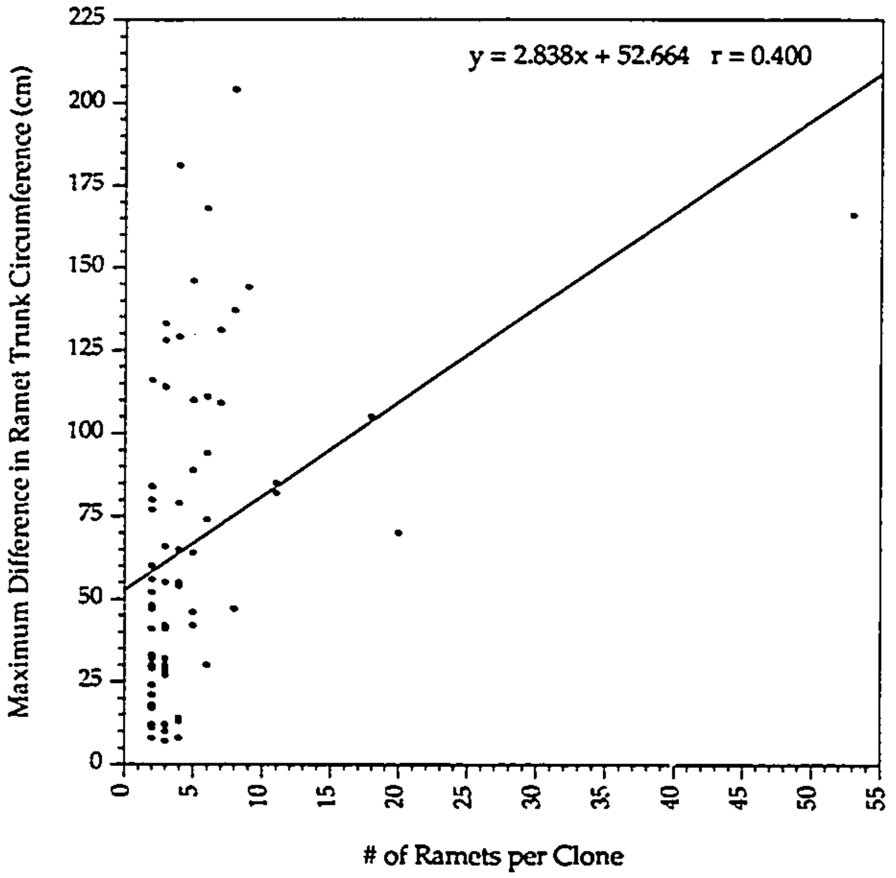


Figure 4-47. The distribution of differences between minimum and maximum ramet-trunk circumferences according to the number of ramets in the clone (N=67).

Table 4-47. Using the X^2 Test of Independence:

a) When the ramets of each putative clone are considered collectively as an individual (genet), is the population's sex ratio equal?

b) If all unsexable genets are male, is the population's sex ratio equal?

a)

	Female:	Male:	Totals:	(Unknown Sex)
Observed:	49	51	100	(15)
Expected (1:1):	50	50	100	

Null Hypothesis: The female to male ratio is 1 : 1.

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 0.04$

df = 1 $\therefore$ at $\alpha = 0.05$, the critical X^2 value = 3.84

Since $0.04 < 3.84$ $\therefore$ fail to reject the Null Hypothesis

Conclusion: The female to male ratio does not differ significantly from 1:1

b)

	Female:	Male + Unknown Sex:	Totals:
Observed:	49	66	115
Expected (1:1):	57.5	57.5	115

Null Hypothesis: The female to male ratio is 1 : 1
(when trees of unknown sex are assumed to be male)

$X^2 = \Sigma \{ (\text{Obs.} - \text{Exp.})^2 / \text{Exp.} \} \therefore X^2 = 2.5130$

df = 1 $\therefore$ at $\alpha = 0.05$, the critical X^2 value = 3.84

Since $2.5130 < 3.84$ $\therefore$ fail to reject the Null Hypothesis

Conclusion: The female to male ratio does not differ significantly from 1:1 when trees of unknown sex are assumed to be male.

Differences in the positioning of male versus female trunks relative to the main river channel may also be attributed to the inflated number of female ramets present closer to the river. To counteract redundancy introduced by closely spaced, identical ramets, the distances for each set of clonal trunks can be averaged to arrive at one position for each genet. When analyzed, these genet distances to the main river channel did not show significant differences between the sexes (Table 4-48). Although repetition of ramet genotypes is responsible for the skewed sex ratio and difference in the positioning of males versus females relative to the channel, such repeats can also exaggerate patterns which already exist in the population. When distance to the main river channel was compared between species-types using the averaged distance for each genet, the species categories were found to differ significantly in their positioning (Table 4-49). Genets from section *Tacamahaca* tended to occur the closest to the river.

4.4 Implications to Cottonwood Regeneration:

In determining clonal relationships, evidence from this investigation makes an important contribution to the understanding of cottonwood regenerative processes. In demonstrating the substantial occurrence of natural asexual regeneration, a large proportion of mature cottonwood trunks was found to be clonally originated. Approximately 88% of all trunks were found to be clonally related to one or more other trunks. A total of 58% of all genetic individuals (genets) were composed of more than one trunk, the largest of which included 53 trunks. Considering that such a large proportion of the population is directly influenced by clonality, there are widespread implications to cottonwood population biology.

Table 4-48. Using the F-Test to choose the proper t-Test for deciding whether male and female genets differ significantly in their mean distances to the main river channel.

F-Test: Two-Sample for Variances

Null Hypothesis: The two samples have the same variance.

	Female Genets	*Male Genets*
Mean	103.09	123.16
Variance	2609.01	1637.83
Observations	49	51
Degrees of Freedom	48	50
F	1.5930	
P (F<=f) one-tail	0.0528	
F Critical one-tail	1.6053	

Decision: Do not reject the Null Hypothesis

Conclusion: The variances are not significantly different, therefore use the following t-Test:

t-Test: Two-Sample Assuming Equal Variances

Null Hypothesis: The two samples have the same mean.

Degrees of freedom	98
t Stat	-2.1822
P (T<=t) one-tail	0.0157
t Critical one-tail	1.6606
P (T<=t) two-tail	0.0315
t Critical two-tail	1.9845

Decision: Do not reject the Null Hypothesis

Conclusion: The sample means do not differ significantly (Male and female genets do not differ significantly in their mean distances to the main river channel)

Table 4-49. Using an ANOVA to determine whether genets from the three different species-categories differ significantly in their mean distances to the main river channel.

SUMMARY:

Categories:	*Count*	*Sum*	*Average*	*Variance*
A to B (*Tacamahaca*)	47	4401.90	93.66	2975.84
AD to BD (intersectional)	44	6158.61	139.97	1255.38
DB to D (*Aigeiros*)	24	2926.85	121.95	479.41

ANOVA: Single Factor

Null Hypothesis: Genets in the three species-categories have the same mean distance to the main river channel.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between categories	49400.79	2	24700.40	13.70	0.0000	3.0773
Within categories	201896.61	112	1802.65			
Total	251297.41	114				

Decision· Reject the Null Hypothesis

Conclusion: Genets in the three species-categories differ significantly in their mean distances from the main river channel. (*Tacamahaca* is the closer to the river than the other categories)

Evidence of clonal-origin in mature trees exists in *Populus angustifolia, P. balsamifera,* and *P. deltoides*. Although marginally significant, there were differences between the species involving the numbers of ramets they produced. Judging from the proportions of clonal versus non-clonal trunks (Table 4-27), the trends suggest that *Tacamahaca* species have the strongest and *Aigeiros* species have the weakest clonal abilities. This difference in clonal capacity might confer an advantage to members of section *Tacamahaca* in environments less conducive to seedling recruitment. Under such conditions, clonal ability would permit woodland regeneration without restriction to seedling recruitment. Indeed, *Tacamahaca* species survive along streams with steep gradients, coarse beds, and constrained channels, where the opportunity for sexual recruitment is less frequent and more constrained. Alternatively, the *Aigeiros* species *P. deltoides,* occurs on freely meandering or braided channels with low gradients and sandy beds, where conditions are more favorable for seedling recruitment, and so asexual regeneration is less necessary for forest maintenance between opportunities for sexual recruitment.

An important point raised by this study involves the capacity of cottonwoods to regenerate even when water levels and competition discourage seedling recruitment. The young saplings observed on the site are likely additions to older clones, because the chance of seedling establishment under the mature canopy is remote, and because most of these trunks were included in putative clones based on phenotypic comparisons. Even following the record flows of 1995 and associated conditions considered ideal for recruitment, no seedlings were observed to colonize these areas. Thus, asexual sprouting represents an alternative regenerative strategy which has less stringent requirements for moisture and competition than does seedling recruitment.

Given the central importance of cottonwoods to riparian forest ecosystems, and their documented decline across the continent, there are management implications for promoting conservation and restoration of cottonwood reproductive mechanisms. Some approaches have focused on seedling reproduction as the only mode for forest regeneration. After recognizing the potential for substantial clonal regeneration, new avenues for management become available. Asexual mechanisms can act as a compliment to the sexual ones, allowing forest replenishment in years or decades where conditions are unfavorable for seedling establishment. By enhancing conditions favoring clonality in cottonwoods, temporary forest replenishment might be accomplished to supplement natural seedling recruitment, conserve extremely sparse stands, or function in erosion prevention.

Considering the superficial appearance of diversity in cottonwood forests, it was surprising to discover that this population of 391 apparent individuals is in fact composed of only 115 genomes, a reduction of over 70%. A young forest would be expected to have a higher proportion of single-trunked seedling-originated individuals. With age, the combined attrition of individuals and expansion of clones would result in overall genotypic reductions. The 70% reduction in the present study hints at a senior age of this site's forest.

Over time, woodland species with strong clonal tendencies would also be expected to dominate the forest's structure. The consequences of such ongoing revisions reach beyond population structure and into genetic complexity. Given a smaller gene pool than originally anticipated, implications range from heightened disease susceptibility, to restricted potential for hybridization. Research in these topics would be well advised to recognize the implications due to cottonwood clonality.

5.0 SUMMARY OF CONCLUSIONS:

5.1 Summary of conclusions for the hypotheses and queries:

Is there evidence of cottonwood asexual recruitment in the study population? Since the environment is homogeneous, the chance is remote that groups of mature siblings would occur in close spatial proximity, and it is unlikely that these siblings would bear close enough resemblance to be confused for clones, the spatially clustered arrangement of individuals with shared heritable characteristics provides evidence of asexual processes. Thus, the first question is answered as, yes.

Is it possible to delineate clonally-related mature cottonwoods according to phenotypic and spatial characteristics? Yes, there are a variety of easily observable physical and phenological traits in cottonwoods available for assessing phenotypic similarity. The population can be successively divided according to dissimilarity in the most heritable characteristics, and a final evaluation of relative proximity will facilitate the final delineation of putative clones.

What trends were detected in the natures of the putative cottonwood clones? Out of the population of 391 trunks, there were only 115 individuals. Of these, 67 consisted of clonal associations. The only significant differences in clonal characteristics detected with respect to the sexes or species-categories were that females had a higher ratio of ramets to single trunks than males, and section *Tacamahaca* had the highest ratio of ramets to single trunks than the intersectional hybrids, and section *Aigeiros*. Additionally, genets from section *Tacamahaca* were found to occur significantly closer to the river than genets of the other two species-categories. It is likely that the large female *Tacamahaca* clones near to the river are largely responsible for these trends.

The clonal tendencies of the population can be summarized with a series of averages. The average number of ramets per clone was 5.12. In total, 58.26% of the population of 115 genets were clonal. The average distance separating two ramets of a clone was 4.07 m. The average diameter of complete clone area was 7.54 m. The average difference in trunk circumference between the smallest and largest trunks of a clone was 67.19 cm. This relatively large value reveals high within-clone circumference variability, and presumably the staggered production of clonal sprouts over time.

What implications do these patterns of clonality have for cottonwood regeneration? The unexpectedly large proportion of mature cottonwood trunks found to be clonally originated has important ramifications for understanding reproductive investment. This high incidence of clonality was observed equally in each of the local cottonwood species and their hybrids, emphasizing the standard nature of the trend. Ramets represent identical copies of one genome and so result in the skewing of the population's genotypic proportions. Such distortion influences population appearance as well as species and sex composition, which in turn affects the nature of seedlings. Sexual and asexual regenerative processes differ substantially in their environmental requirements and adaptive advantages, so the recognition of considerable clonal contribution will have diverse consequences, most notably pertaining to population biology and system management.

5.2 Generalizations, Implications, Recommendations

To compose accurate generalizations, the study site's situation must be representative of the region of interest. Specifically, the weir-island population must be representative of the rest of southern Alberta. Although riparian cottonwood woodlands in this region are extensive and widely variable, stable forests of moderate size with a spatial clustering of phenotype, and a similar age, would be expected to resemble the study site in patterns of clonality. Anywhere within this locality, a quick survey of select phenotypic characteristics should lead to a reasonably accurate assessment of clonality based on principals from the present study site.

The phenotypic and phenological characteristics identified in this study vary in their utility for delineating clones. The value of a character is proportional to the directness of its link to the genotype. Accordingly, sex was decided to be the most useful, followed closely by species-type as determined from general leaf shape. The phenological characters involving timing of flowering, leaf-flushing, and leaf-senescence, were of intermediate value when their potential for environmental influence and the time-consuming nature of their observation were considered. Finally, spatial proximity of similarly characterized trunks provided a simple convention for the reduction of potential clone groups. Trunk architecture was found to be of little use since the information it offered was redundant with the determination of species and complicated by tree age. Due to the combined strength of sex, species-type and phenology, the two remaining groups of characteristics: mite gall abundance and the six leaf dimensions, were only used to reinforce the already established groupings.

To apply these findings to other sites, it should be possible to detect clonal patterning by conducting general surveys of the key traits from the present study. The first traits of choice would include sex and species-type within their spatial contexts. Such surveys are time and labour intensive and some characteristics are only observable during certain seasons; sex can only be physically determined in early spring, while species estimations are more generally available from foliar characteristics. Superficial surveys could be conducted for the characters which are observable at a distance. General tree appearance and differences in the phenologies of leaf flushing and senescence could be documented using aerial photography to give a general impression of spatial clustering, and thus lead to an estimation of clonality. However, denser forests might feature interdigitating clones, which would not be discernible using such methods, and unless there is high photographic detail, closely-spaced, multiple-trunked clones might be mistaken for large, single-trunked individuals.

The present investigation has revealed an unexpected degree of asexual regenerative strategy in riparian cottonwoods. It is strongly recommended that the clonal contribution in other regions be similarly investigated. With concern rising over declines in riparian forests, new information addressing the regenerative capability of cottonwoods has direct implications for management strategies. Since clonal mechanisms appear to compliment sexual reproduction by maintaining vegetative growth within groves, managers might choose to enact regimes favoring asexual, as well as seedling, regeneration. Such an approach would be especially useful in managing rapidly declining mature cottonwood groves which lack sufficient seedling succession to maintain a sufficient forest population structure.

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