

Crown development of a clone of *Populus tremuloides* exhibiting "crooked" architecture and a comparison with wild-type trees

William R. Remphrey and Linda P. Pearn

Abstract: *Populus tremuloides* Michx. (trembling aspen) is a tree species native to much of North America and is normally ascribed to the architectural model of Rauh, characterized by an excurrent crown structure with a central main stem and orthotropic branches. A mutant clone of trembling aspen is located near Hafford, Saskatchewan, exhibiting an architecture with crooked and twisted tree trunks. It was the objective of the present study to determine how the architectural development of the crooked clone differed from the wild type. In a study conducted over a 5-year period, four mutant trees were compared with four young wild-type aspen in the Winnipeg, Manitoba, area. Based on detailed quantitative data, it was determined that the architecture of the crooked clone of aspen differs greatly from the wild type. The trees are built by the continuous superposition of vigorous relay shoots with a mixed orientation, that is, shoots that take over the main growth of the tree, and have a more or less upright basal part and a horizontal to pendulous distal part. The development of the crookedness starts with the bending of the relay shoots, mostly in relation to the gravitational direction, which is followed in the subsequent years by various gravimorphic responses. In particular, the longest lateral shoots on a parent relay shoot occur in the middle regions, and the tip of the parent relay shoot generally loses vigour over time. The parent shoot may die back to the junction with a daughter relay shoot, causing a sharp bend at that point. Moreover, the divergence angles of relay shoots with the parent shoots were shown to be greater than in wild-type aspen, and this appears to exacerbate the crookedness. The new relay shoot may actually grow back towards the centre of the crown, opposite to the direction of growth of the parent. The results of this study demonstrate how a quantitative change in one architectural character can set in motion a series of developmental processes that result in a vastly different crown structure from the wild type.

Key words: *Populus tremuloides*, trembling aspen, architecture, crooked clone.

Résumé : Le *Populus tremuloides* Michx. (peuplier faux-tremble) est une essence indigène qu'on retrouve dans une bonne partie de l'Amérique du nord et qui se conforme normalement au modèle architecturale de Rauh, caractérisé par une structure de la couronne ouverte, avec une tige centrale principale et des branches orthotropes. Près de Hafford, en Saskatchewan, on trouve un clone mutant de peuplier faux-tremble dont l'architecture montre des courbures et des torsions des troncs. Les auteurs ont cherché à déterminer comment le développement architectural, chez ce clone tordu, diffère de celui du type sauvage. Une étude ayant duré 5 ans a permis de comparer quatre arbres mutants avec quatre jeunes peupliers faux-tremble de type sauvage, dans la région de Winnipeg au Manitoba. Les données quantitatives montrent que l'architecture du clone tordu du peuplier faux-tremble diffère grandement de celle du type sauvage. Les arbres se développent par superposition continue de tiges à relais vigoureuses avec une orientation mixte, tiges qui deviennent la tige principale de l'arbre, et qui ont une partie basale plus ou moins dressée et une partie distale allant d'horizontale à pendulée. Le développement de la torsion commence avec la courbure des tiges à relais, surtout en relation avec la direction gravitationnelle, ce qui est suivi, au cours des années subséquentes, par diverses réactions gravimorphiques. En particulier, les tiges latérales les plus longues sur une tige à relais mère apparaissent dans les régions médianes, et l'apex de la tige à relais mère perd généralement de la vigueur avec le temps. La tige mère peut dépérir jusqu'à la jonction avec une tige à relais fille, causant une courbure prononcée à ce point. De plus, on constate que les angles de divergence des tiges à relais avec les tiges mères sont plus grands que ceux des peupliers faux-tremble de type sauvage, et que ceci accentue la courbure. La nouvelle tige à relais peut en fait croître inversement vers le centre de la couronne, en direction opposée à celle de la croissance de la tige mère. Les résultats démontrent comment un changement quantitatif dans un caractère architectural peut déclencher une série de processus développementaux conduisant à une structure de couronne largement différente de celle du type sauvage.

Mots clés : *Populus tremuloides*, peuplier faux-tremble, architecture, clone tordu.

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Introduction

The classical perception of tree crown architecture is that of one or more main stems or trunks with lateral branches growing horizontally or at some angle upwards. However, Hallé et al. (1978) described several types where the branches may arch and the tips point at an angle downwards (e.g., various apples and plums) and more extreme forms whereby the most recent increments grow downwards and may possibly hang straight down (e.g., *Salix alba* 'Tristis', *Betula pendula*, and *Larix decidua* 'Pendula'). Many of these pendulous types have been propagated for use in ornamental gardens. There have also been plants described in which the branches appear to be significantly twisted or bent in various ways. One notable example that has been extensively studied is a population of twisted beech (*Fagus sylvatica* var. *tortuosa*) known as "tortillards" growing in Verzy, France (Thiébaud et al. 1992, 1993, 1998). These twisted beeches were described in Denmark in the early 1900s (Oppermann 1908). There have been casual observations of other twisted woody plants, for example, a grove of twisted black cherry in the "land of the crooked trees" in Massachusetts and a clonal grove of larch in Scotland described as follows: "the tree sports a mass of twisting and contorted branches which weep to the ground and take root. Increasing in ever-expanding circles of serpentine branches, this one tree covers a vast area of ground. It is well-worth a visit to marvel at its crazy architecture and relentless survival strategy" ([http://www.treefestscotland2002.org.uk/website/FavouriteTree.nsf/\(HeritageByName\)/7B2069DCA5F168A580256B820056DCEF](http://www.treefestscotland2002.org.uk/website/FavouriteTree.nsf/(HeritageByName)/7B2069DCA5F168A580256B820056DCEF); accessed December 18, 2002).

At least since the 1940s, a population of trembling aspen (*Populus tremuloides* Michx.) with a crooked architecture was observed growing at the edge of an agricultural field near Hafford, Saskatchewan. For years, local residents have speculated on the cause of this growth form: everything from soil contamination to effects of a meteorite crashing into the area and altering the development of the trees (Gossner 1999). While environment can have significant effects on tree architecture, for example, the twisted "Krummholz" vegetation typical of trees growing in windswept areas (Hallé et al. 1978), closer examination and vegetative propagation of the crooked aspens have revealed that this population is a clone derived from a single genotype and the likelihood is that the crooked trait stems from a genetic mutation (data not shown). This conclusion is supported by others who have suggested that the crookedness is the result of a genetic modification in one of the earliest trees in the stand (http://www.virtualsk.com/current_issue/crooked_trees.html; last accessed December 18, 2002). Accordingly, because the trait can be propagated, it has little to do with location or soil factors.

Casual observation of the crooked aspens reveals that a major factor contributing to the crooked form of the mutant aspens is the bending of shoots to a more horizontal or pendulous orientation. Such bending has been attributed to "gravi-epinastic effects" (Hart 1990) in which endogenously controlled differential growth acts to force a branch to grow downwards. This usually counteracts the gravitropic response for shoot tips to grow upwards. Although bending

partially explains the crookedness, there appear to be other architectural mechanisms involved in creating the structure. In the tortillard beeches, the twisted architecture appears to be related to a combination of weakened apical control, increased sympodial branching, a more plagiotropic orientation of shoots, and repeated reiteration of the architectural model (Thiébaud et al. 1993). Training shoots to a horizontal orientation has been shown to result in reduced extension growth and weaker apical control in several species of fruit trees, often resulting in more shoots developing from the upper side compared with the lower side (Wareing and Nasr 1961; Hart 1990). Such a modification in growth form in response to gravity has been termed gravimorphism (Wareing and Nasr 1958) and it usually refers to the effects other than orientation. This raises the possibility that a modification in the orientation of shoots may be a prerequisite for additional gravimorphic responses contributing to the development of the crooked architecture in the mutated aspens.

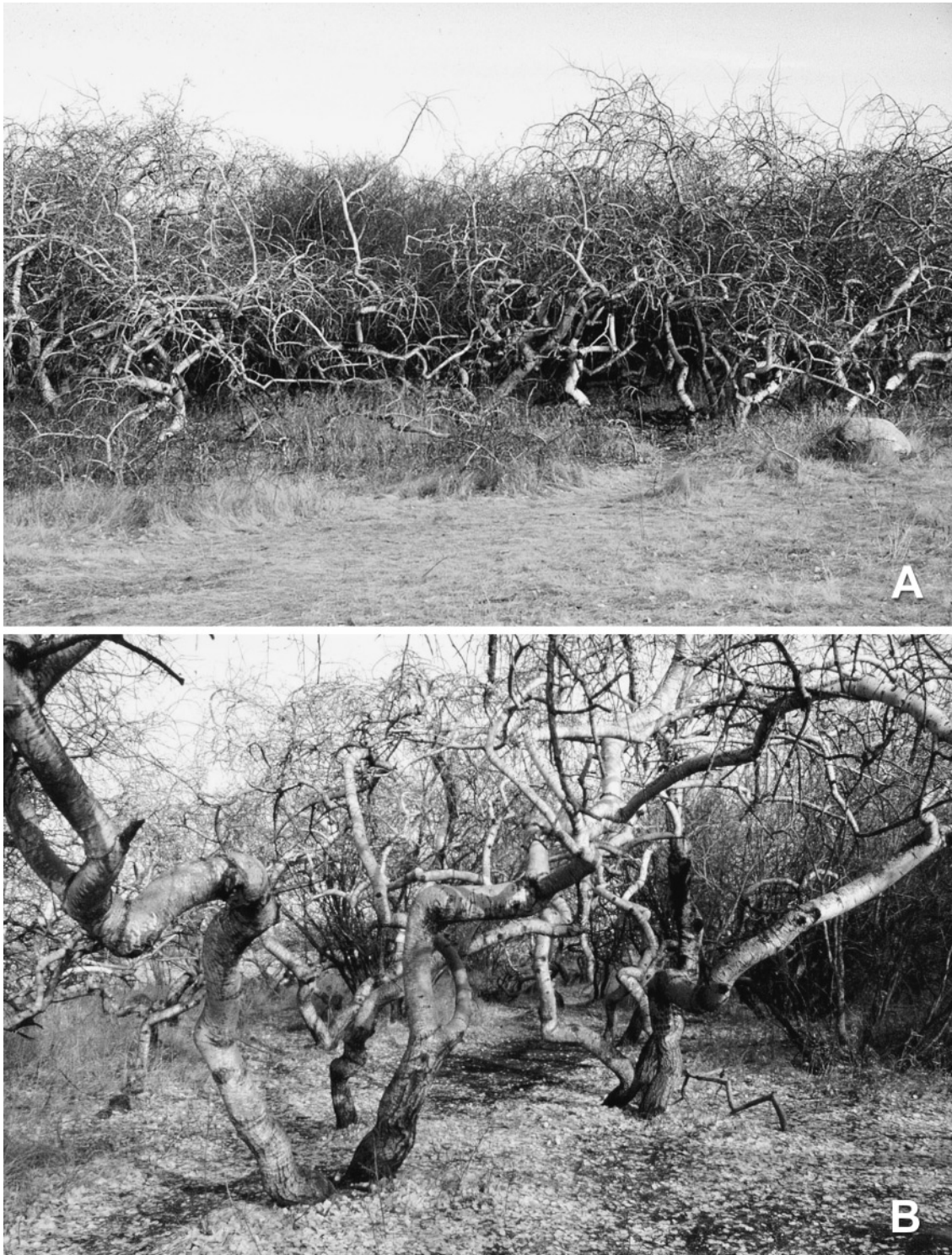
Woody plants with pendulous branches have been recognized for a long time, including early descriptions in the literature of plants with mixed axes (e.g., Rauh 1939; Champagnat 1947). With the exception of the tortillard beeches (Thiébaud et al. 1993), there is little quantitative architectural information on such forms. Thus, the main objective of the present study was to use a quantitative architectural approach (see Remphrey and Prusinkiewicz 1997) to determine how the crooked form develops in the Saskatchewan clone and compare this architecture with "normal" wild-type aspen. A secondary objective was to interpret the architecture in relation to the concepts of gravitropism and gravimorphism. This analysis involved obtaining measurements over consecutive years of shoot lengths, angles, branching location, and branching frequency in the crowns of crooked aspen trees as they developed in the field.

Materials and methods

Study materials

Part of the plant material for the present study was obtained from a male clone of native *P. tremuloides* that is located at the edge of a farm field approximately 20 km northwest of Hafford, Saskatchewan (Fig. 1). This clone is characterized by having distinct "crooked" stems. In October 1992, 18 root sprouts (suckers) less than 1 m tall were harvested from the edge of the clone along with some soil about the roots. The root systems were packed in peat moss and placed in plastic bags for transport back to the University of Manitoba. Extra pieces of root exposed during the harvesting procedure were also collected and used to propagate crooked trees for the present study. The root pieces harvested from the clone were stored in damp peat moss in plastic bags at 4°C until February 1993. From storage, the root pieces were pretreated in moist peat moss in a sealed plastic bag at 22°C for 2 weeks (Vanstone et al. 1982). One end was then trimmed and dipped in 0.1% indole-3-butyric acid rooting powder and each root piece was planted into a 10-cm pot in a soil-less mix. These were put into a mist chamber with bottom heat for 2 weeks by which time, roots had formed and shoots were emerging at the surface. The humidity was gradually reduced and the plants were moved

Fig. 1. Crooked *Populus tremuloides* located near Hafford, Saskatchewan, as it looked in October 1992. (A) View of the stand showing the relatively low stature of the trees. (B) Closer view of trees showing how the large main axes are crooked.



to a greenhouse. After 3 months of growing in the greenhouse, they were moved to cold frames outdoors and 1 month later planted in a 3-m grid in the field. The trees were beginning to exhibit the crooked trait when transplanted. The trees were watered and fertilized with 10:52:10 water-soluble fertilizer (rate 6.6 mL/L) at the time of trans-

planting. To help control weeds and facilitate access, a fescue grass was established around the plants in the third year after transplanting.

To compare architectural traits of the crooked aspen with wild types, four 6-year-old trembling aspen trees were selected randomly from the edge of a bluff on the outskirts of

Winnipeg in late fall, 2001. The selected trees were suckers that were probably derived from the same clone, but it was not possible to verify this. For measurement, each tree was removed from the original site, brought into the laboratory, and oriented the same as it had been in the field.

Crown architecture measurements

Crooked aspen

In the autumn of 1996, two 1996 shoots in the upper crown arising from the same 1995 shoot and judged to be major axes involved in constructing the crown were selected in each of the four experimental trees and tagged. These shoots were vigorous, similar in size, and originated from the upper side of the parent shoot. Beginning with baseline measurements of 1995 parent shoots, detailed architectural measurements were obtained in 1996 and 1997 for both daughter shoot complexes initiated in 1996 (see Table 1 and Fig. 2 for an explanation of the variables measured). Detailed measurements were continued for selected shoots over successive growing seasons until 1999 for only one of the 1996 shoots. A system of tagging was developed to keep track of all shoots being observed.

The selection process of shoots to be measured over successive years was as follows. In 1997, detailed measurements were made on all daughter shoots judged to have potential in continuing to build the main axes of the crown (termed relay shoots (Table 1)) and minor measurements were done on the other daughter shoots. In 1998, two classes of 1997 shoots were selected to follow subsequent development: (i) vigorous relay shoots and (ii) shoots judged previously as potential relay shoots but beginning to lose vigour. Because of the exponential increase in the number of shoots formed in 1998, a subsample of two or three shoots judged to be vigorous relay shoots was selected. In 1999, this process was repeated except that shoots judged previously as potential relay shoots but now likely to form minor branches were chosen in addition to the above two types of shoots.

In the fall of each year, all daughter shoots arising from selected shoots were measured. Measurements for all daughter shoots included length, location on parent measured from the base, position of origin around the parent (Table 1; Fig. 2A). Diameter of shoots, except for morphological short shoots, was also obtained 1 cm from the base. To facilitate the measurement process, all measurements for this data set were obtained in the autumn after the leaves had abscised.

For a shoot designated as a relay shoot, the orientation morphology was measured by dividing the shoots into four segments based on the main points where the orientation with respect to gravity changed. The lengths and elevation angles of the secant of each segment were measured (Fig. 2B). In addition, the planar bending angle was measured as the angle between successive segments measured in the horizontal plane (Table 1; Fig. 2C).

To assess the effect of shoot dieback and shedding on architecture, measurements were commenced in the autumn of 1998. The diameters of all 1997 and 1998 lateral shoots arising from vigorous measurement shoots were obtained as an indicator of side branch vigour and ultimate contribution to the architecture. In addition, the diameter of the main mea-

Fig. 2. Diagrams indicating several of the architectural variables measured (see Table 1 for an explanation of the variables). (A) Side-view profile of crooked *Populus tremuloides* relay shoots showing the divergence angle (α) between a daughter relay shoot (D) and its parent shoot (P). (B) Side-view profile of crooked *P. tremuloides* relay shoots showing segments (1 to 4 from the base) of a daughter relay shoot on its parent shoot and the angle of elevation (β) of segment 2. (C) Plan view of crooked *P. tremuloides* relay shoots showing segments (1 to 4 from the base) of a daughter relay shoot, its parent shoot, and a sample planar bending angle (γ) between successive segments of the daughter shoot. (D) Side-view profile of wild-type *P. tremuloides* shoots showing the angle of termination (δ) between a daughter lateral shoot and its parent shoot that is a component of the main stem axis.

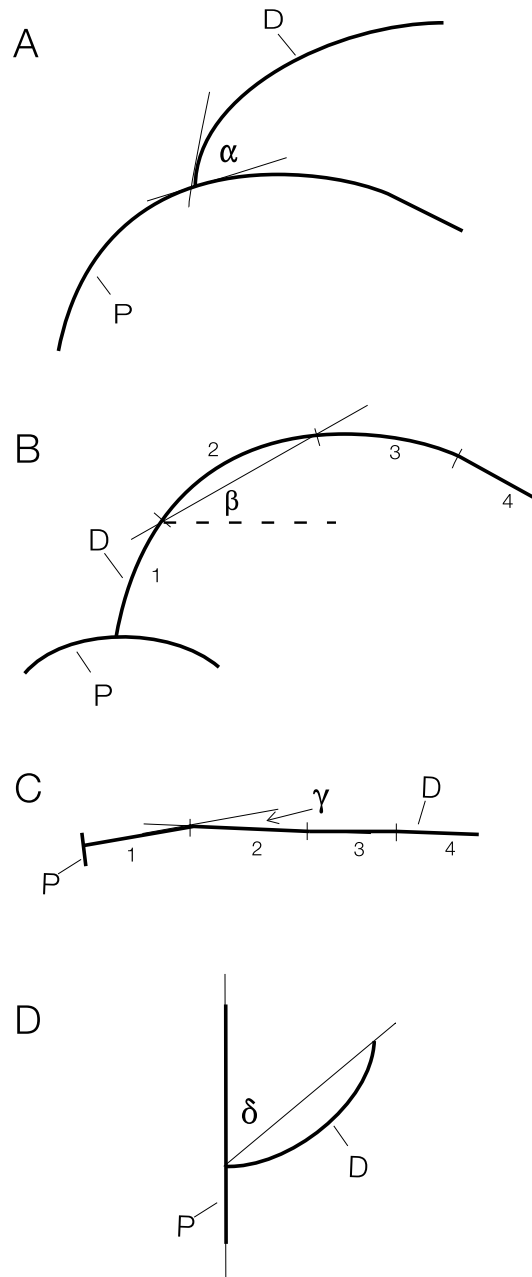


Table 1. Terminology and description of variables measured in detailed architectural data sets (see Fig. 2 for a diagrammatic representation of several of the variables).

Term or variable measured	Definition or explanation
Angle of termination	Angle between parent shoot axis and the secant between the base and tip of the daughter shoot on wild-type trees (see Nelson et al. 1981)
Axis	Describes the main line or direction of growth of a plant. It may be used to refer to a branch or the main stem of a tree
Daughter shoot	A shoot developing on a parent shoot in the next generation
Diameter of shoot	The diameter was measured 1 cm from the base of the shoot to the nearest 1/100 mm using digital vernier calipers
Divergence angle of axillary shoots	Angle between parent shoot axis (tangent of the arc of crooked shoots) and the initial axis direction of the axillary daughter shoot (Davidson and Remphrey 1990). This angle is sometimes referred to as angle of origin (Nelson et al. 1981) and was measured using a modified protractor
Location of daughter shoot along parent shoot	Measured from the base of parent to junction with daughter shoot
Nodal location of daughter shoot	Node number counted from the base of the parent. Nodes where the bud aborted or remained dormant were included in the sequence
Number of nodes	Total number of nodes per parent shoot and per segment
Parent shoot	A shoot whose terminal and axillary buds have expanded into shoots in the next growth flush
Planar bending angle of segments	Angle between the axis of a segment and the projected axis of the previous segment. This angle recorded bends that occurred in planes other than those related to gravity
Position of origin around the parent	Measured on leaning or pendulous parent shoots according to numbers on a clock face: top is 12 and bottom is 6. These values were translated into a linear sequence, where 1 is the top of the parent and 5 is at the bottom
Relative distance to daughter shoot	Distance of daughter shoot from the base of parent expressed as a percentage of the total parent shoot length
Relay axis	Axis formed by portions of relay shoots (see Hallé et al. 1978)
Relay shoots	Shoots that take over the main growth of the tree, involved in forming axes. Such shoots may or may not extend the crown in height
Segments	To capture curvature and bending of shoots, each shoot was divided into four segments that best fit the arc of the shoot. The end of each segment was at a node and the node number for the end of each segment was recorded
Segment angle of elevation	The angle of elevation with respect to gravity was measured for each segment by measuring the elevation of the secant of each segment. This angle was obtained using a carpenter's tool for measuring roof pitch
Segment secant length	Length of the secant relative to the ends of the arc of each segment
Shoot	Annual increment of extension growth arising from an overwintering bud and ending in a terminal overwintering bud. Length measured from base of shoot to base of the terminal bud

surement shoot was obtained on either side of the laterals to assess where the energy shift occurred from terminal growth to one or more of the laterals. The specific fate of the terminal portion the major measurement laterals was also assessed. This was done in two ways: (i) measuring the amount of growth of successive terminal shoots and (ii) assessing the extent of dieback from 1998 to 2000.

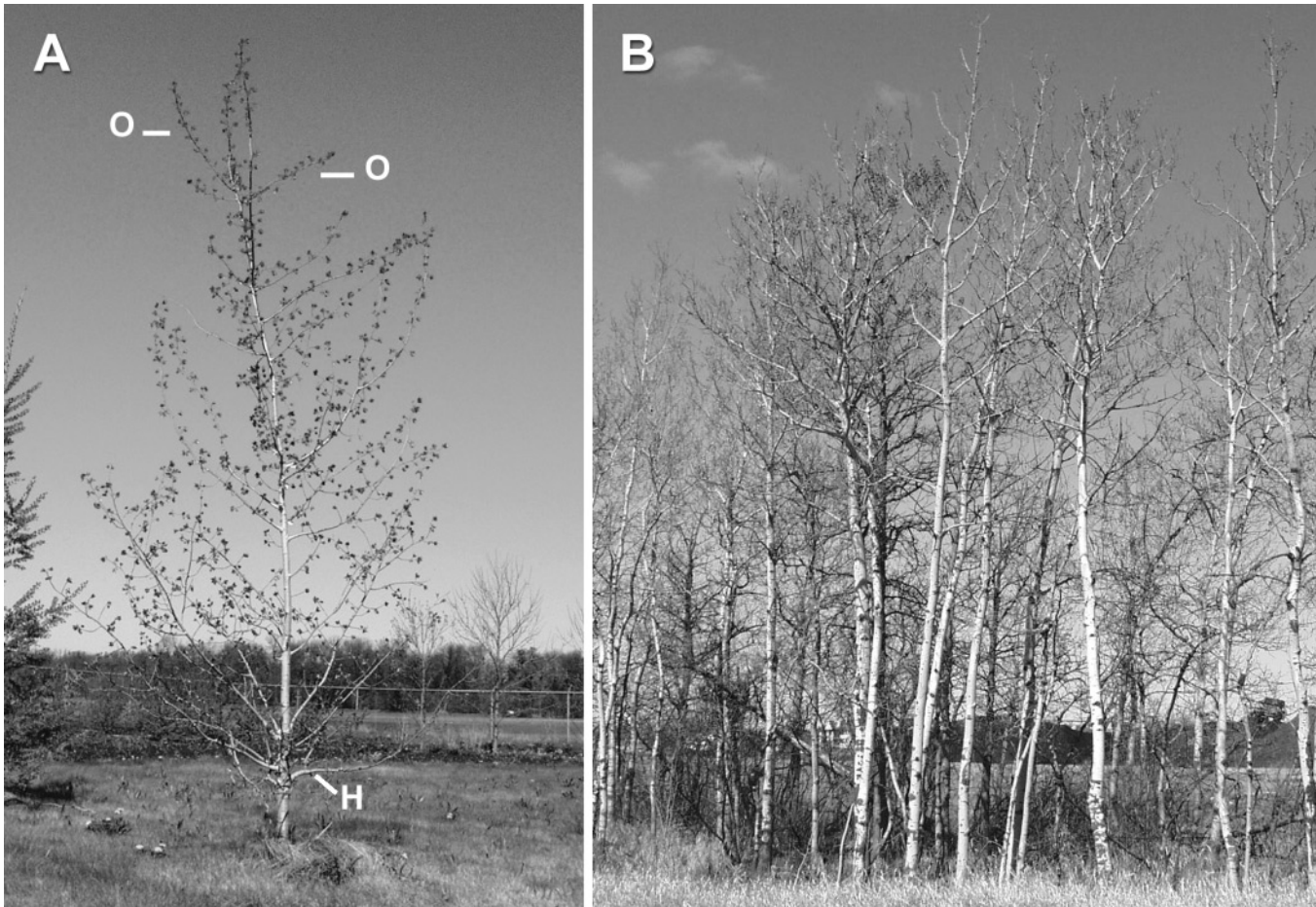
In 2001, the crowns of the crooked trees were randomly

sampled to assess the number of relay shoots developing from each major parent shoot from 1996 to 2000.

Wild-type aspen

On each of the four wild-type trees, the main stem shoots from 1998 to 2001 and all lateral shoots arising from them were measured. In addition, a first-order branch initiated in 1999 was similarly measured. Measurements included

Fig. 3. Wild-type *Populus tremuloides* trees. (A) Single specimen, 9 years old, transplanted from the wild in 1995 showing the excurrent form. Note the typical oblique orientation of lateral shoots (O) on the leader and the more or less horizontal lateral shoot (H) that may have reoriented as the branch aged. (B) Stand of excurrent trees located on the outskirts of Winnipeg, Manitoba.



length, location along and around the parent similar to the crooked trees, diameter, divergence angle, and angle of termination (see Table 1 and Fig. 2D for an explanation).

Data analysis

To determine quantitative architectural patterns in relation to location parameters, data were analyzed using standard statistical techniques including correlation analysis, linear regression, and χ^2 tests of independence.

Results

Comparison of wild-type and crooked aspen

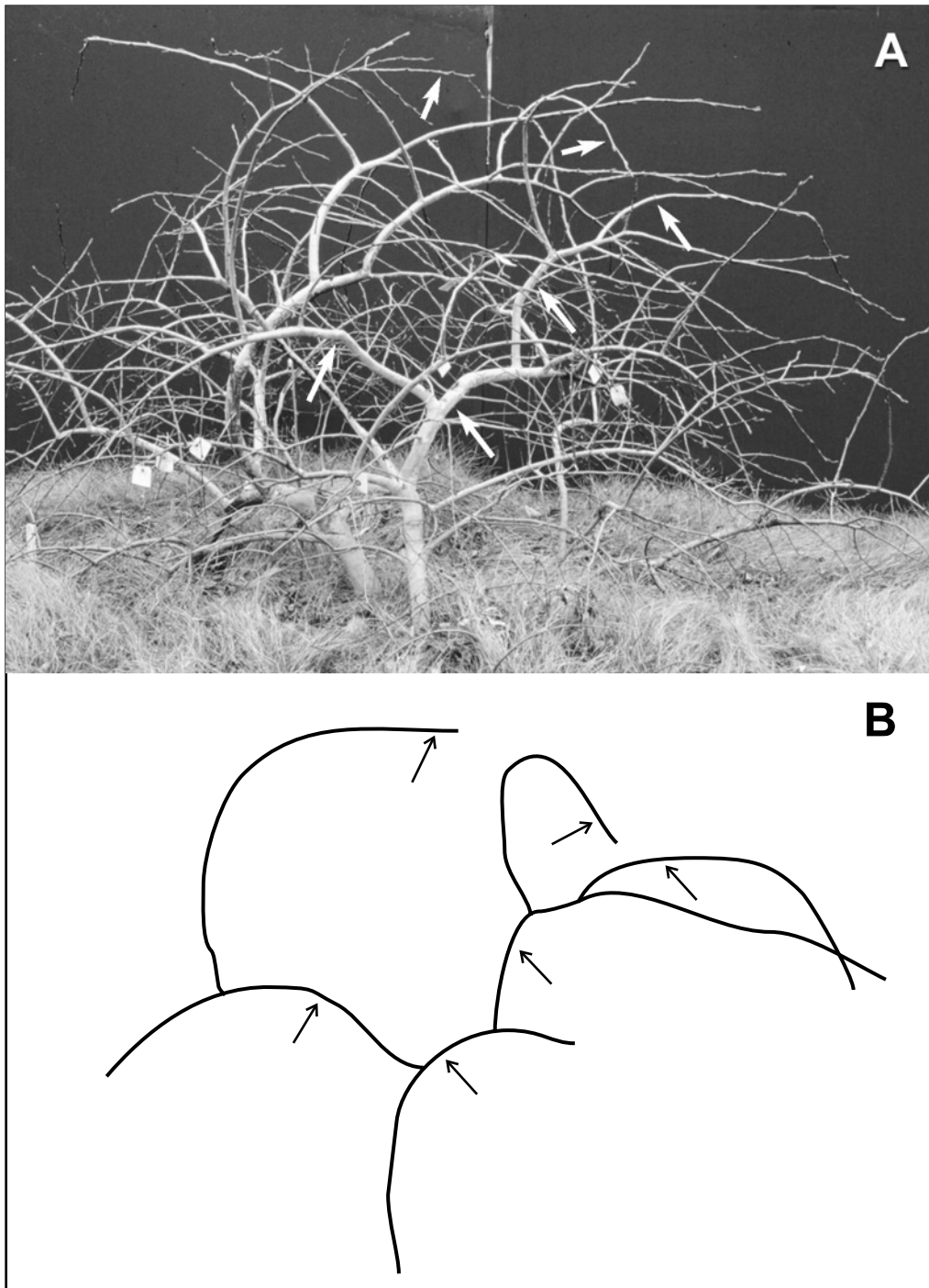
General architectural pattern of development

In wild-type trembling aspen, the crown has a more or less distinct main stem and subordinate branches, at least in young trees, and exhibits a typical excurrent form (Fig. 3). Each shoot contributing to the main stem grows more or less orthotropically (Fig. 3A). The result is a distinctive leader shoot that contributes to continuous height growth. The lateral shoots on the leader tend to be held at an oblique angle with a mean angle of termination of $48.8 \pm 1.4^\circ$. These shoots typically bend upwards toward the tip (Fig. 3A).

There was no relationship between angle and the location of the lateral shoot along the parent shoot.

The architecture of the crooked clone of aspen differs greatly from the wild type, as it is built by the continuous superpositioning of vigorous relay shoots that tend to have a mixed orientation (Fig. 4). A typical renewal relay shoot has a more or less upright basal portion and a somewhat horizontal to the pendulous distal portion. This results in slow height growth (Figs. 1A and 5) because it is based on the upright, basal portion of the renewal shoot, which is often relatively small (Figs. 6 and 7). Such renewal shoots are distinctly curved resulting from several orientation changes that occur in relation to the gravitational direction during the expansion period (Table 2). On average, the distal three segments, comprising almost 80% of the length of shoots with potential to be major relay shoots, were plagiotropic to pendulous. This portion encompassed about 60% of the nodes (Table 2). However, there was considerable variability and there were cases where the putative relay shoots had distal portions that remained more upright. In any event, the tendency was that the longer the relay shoot, the more pendulous the distal end and thus the more curved the shoot ($Y = 30.29 - 0.094X$, where Y is the elevation angle of the distal segment and X is the length of the shoot; $P < 0.0001$, $R^2 = 0.21$, $n = 87$ shoots). Conversely, some of the vigorous

Fig. 4. Crooked *Populus tremuloides* measurement tree when it was 6 years old. (A) Photograph showing how the superpositioning of curved relay shoots (arrows) builds the crown. Note that there is more than one main stem emerging from the ground. (B) Schematic representation of selected axes of the tree in Fig. 4A showing how the “crookedness” develops. Note the increase in the number of relay axes as the crown develops. The arrows point to the corresponding shoots labelled in Fig. 4A.



shoots interpreted as potential relay shoots arose from the sides of the parent axis, and these tended to be more horizontal near the base and pendulous distally. Although such shoots added to the frame of the tree, they were not involved in height growth. Occasionally, such shoots gave rise to new relay shoots with an upright component in the following year. Similar to wild-type aspen, smaller shoots arose from

various locations around and along parent shoots. These shoots were relatively straight.

Besides the formation of pendulous shoots, shoot growth direction often changed in the horizontal plane as well. However, there was considerable variability in the amount of bending in the horizontal plane; some shoots bent very little between segments, while others bent at angles of over 50°

Fig. 5. A 9-year-old crooked *Populus tremuloides* on the right (1990 mm in height) and a 9-year-old wild-type tree (4855 mm in height) transplanted from the wild in 1995 (tree in Fig. 2A) on the left showing the variation in architecture and the rate of height growth. These two images were derived from the same photograph, but because there was a considerable gap between the trees, the space between has been cropped out. **Fig. 6.** Closeup of a sequence of three relay shoots (arrows) of crooked *Populus tremuloides* showing varying degrees of uprightness of the basal portion in successive years of growth; 1 = 1999, 2 = 2000, 3 = 2001. Note the 2001 relay shoot (B) that bends back towards the origin of the parent. **Fig. 7.** Closeup of distinctly upright basal portions of relay shoots (arrows) of crooked *Populus tremuloides* that are forming the relay axes. **Fig. 8.** Current-year relay shoot of crooked *Populus tremuloides* viewed from above showing the point of curvature (arrows) in planes other than the vertical. The origin of the shoot (O) is indicated. **Fig. 9.** Example of a crooked *Populus tremuloides* parent relay shoot (P) that gave rise to two relay axes (R1 and R2). Note how the distal end of the original parent relay shoot (arrow) has declined in vigour to the extent that it is virtually dead back to the junction with the most distal daughter relay shoot. **Fig. 10.** A 2-year-old crooked *Populus tremuloides* specimen showing the formation of more than one relay shoot (arrows) in the second year on the original curved parent axis (A).

Table 2. Mean (\pm SE) elevation angles, secant lengths, secant lengths as a percentage of cumulative length of secants for each shoot, number of nodes per secant, and number of nodes per secant expressed as a percentage of the total number of nodes per shoot for each segment of relay shoots in *Populus tremuloides*.

Segment characteristic	Segment number from base of shoot			
	1	2	3	4
Elevation angle (degrees above or below horizontal)	36.9 \pm 2.8	17.8 \pm 3.2	-5.9 \pm 3.8	-22.0 \pm 4.7
Length of secant (mm)	111.3 \pm 7.5	128.9 \pm 7.2	159.8 \pm 9.8	137.9 \pm 8.5
Percentage of total secant length	20.9 \pm 1.0	24.2 \pm 1.0	29.6 \pm 1.1	25.4 \pm 1.2
Number of nodes	10.4 \pm 0.3	4.6 \pm 0.2	5.1 \pm 0.2	6.7 \pm 0.4
Percentage of total nodes	39.4 \pm 0.8	17.4 \pm 0.7	19.1 \pm 0.7	24.2 \pm 0.9

Note: A minus sign indicates that the shoot is orientated at an angle below the horizontal.

Table 3. Frequency table for the number of shoots per *Populus tremuloides* parent that were interpreted to be relay shoots in relation to the year that the shoots were formed.

Year of formation	Number of relay shoots as in 2001				
	1	2	3	4	5
1997	3	2	0	0	0
1998	4	3	1	0	0
1999	1	5	4	0	0
2000	2	5	2	2	0
2001	0	2	0	2	1

Note: The frequency counts were made in spring, 2002; χ^2 test of independence between number of relay shoots and year of their formation: $\chi^2 = 25.61$, $P = 0.059$.

(Fig. 8). The mean (\pm SE) planar bending angle between the first two and second two segments of relay shoots was 6.73 ± 0.72 and $6.20 \pm 0.60^\circ$, respectively. The mean angle was slightly greater for the bend of the most distal segment ($8.58 \pm 1.09^\circ$).

Frequently, in the crooked aspen, more than one axillary shoot on a parent functioned as a relay shoot and the result is typically a crown with no clear central leader axis (Fig. 9). In the year when the daughter shoots were first produced, several appeared to have potential to function as relay shoots. However, by the time they are 3 years old or more, the number of these shoots interpreted to be relay shoots tended to decline (Table 3). This decline was correlated with the observation that certain shoots lost vigour after the first year and became subordinate branches. This was demon-

strated by the rate of increase in diameter. Those shoots that continued to function as relay shoots increased in basal diameter by 2.5 times after 2 years; conversely, those downgraded to a less vigorous, subordinate branch category increased in diameter by only 1.5 times. In any event, after 3 years, 35% of parent shoots had one renewal relay axis, 43.5% had two relay axes, and 21.5% had three relay axes ($n = 23$ parent shoots). This multibranch aspect of the architecture became evident early in the development of the tree and was observed in the second season in plants propagated from tissue culture (Fig. 10). Coupled with this, new sucker shoots may arise near the base of the plant, thus reiterating the process of crown development, and the result is an almost shrub-like appearance to the tree (Fig. 4A).

Branching patterns: quantitative differences in apical control

Developmentally, the main stem and branches of wild-type trembling aspen are constructed by a monopodial branching pattern with relatively strong apical control, whereby the main leader is more vigorous than the lateral long shoots and the laterals tend to become progressively shorter with distance from the tip of the parent shoot (Fig. 11). However, shorter shoots are frequently interspersed with the longer ones near the tip. On young trees, approximately 30% of the shoots on the leader parent shoot develop into short shoots 50 mm or less in length. Frequently, the terminal buds abort and are typically replaced by one upper lateral forming a "bayonet joint" (Fig. 12).

In the crooked aspen, the terminal bud and axillary buds along the shoot of a major axis begin to expand in spring as in wild-type trembling aspen. However, it becomes clear

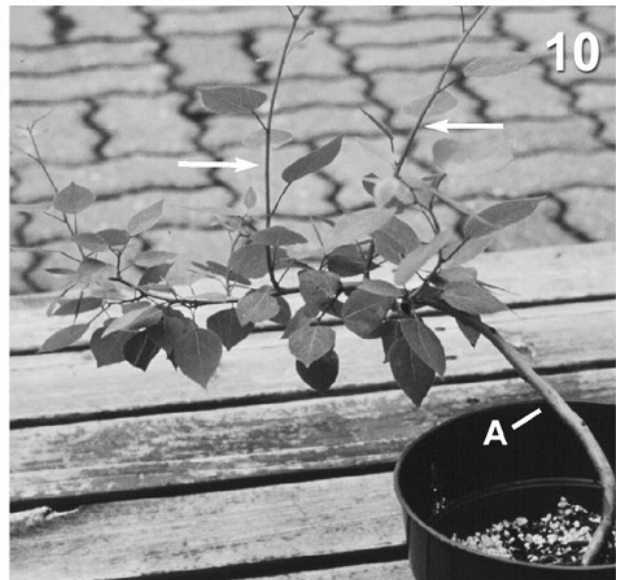
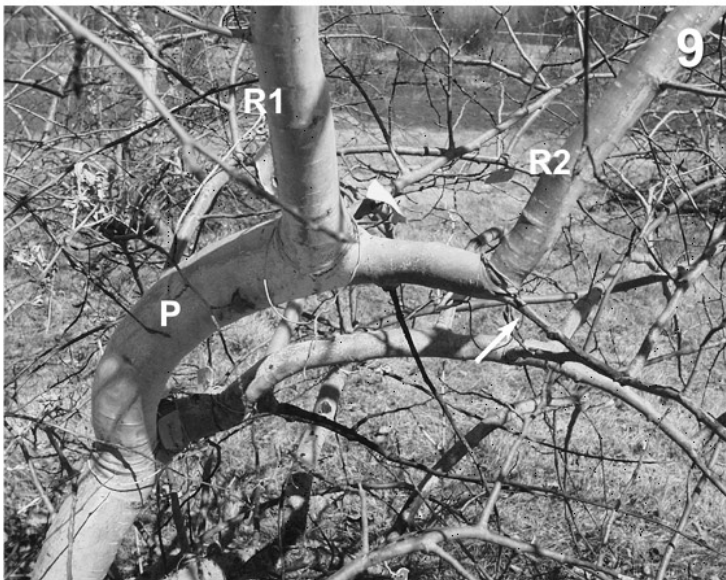
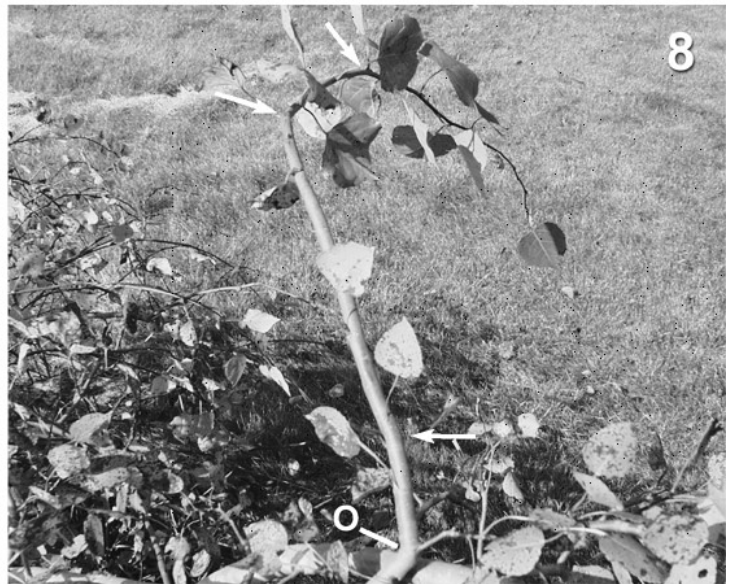
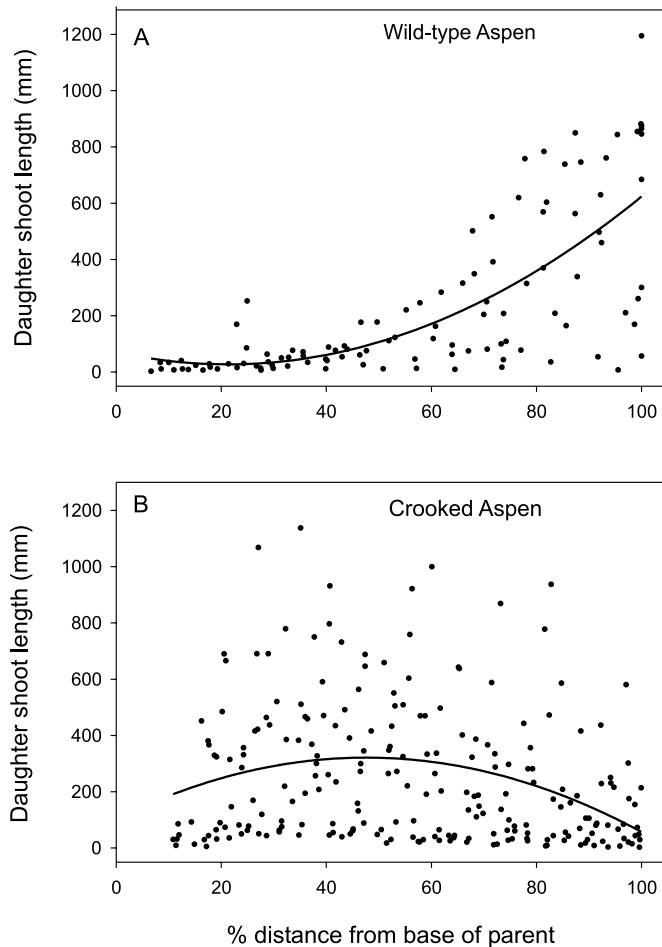


Fig. 11. Relationship between length of daughter shoots and location along a parent shoot. (A) Polynomial linear regression for main stem shoots of wild-type *Populus tremuloides*: $Y = 71.07 - 4.11X + 0.096X^2$, where Y is shoot length and X is the relative distance from the base (see Table 1 for an explanation) ($P < 0.0001$, $R^2 = 0.53$, $n = 108$ daughter shoots). (B) Polynomial linear regression for daughter shoots on parent relay shoots of crooked *P. tremuloides*: $Y = 103.24 + 9.16X - 0.09626X^2$ ($P < 0.0001$, $R^2 = 0.09$, $n = 224$ daughter shoots).



very early that quantitative expression of architectural parameters deviates from that of the wild-type aspen. In the crooked aspen, the terminal and distal lateral shoots are not necessarily the longest shoots, although on occasion the terminal or upper laterals may be as long as the putative daughter relay shoot further back. Typically in the crooked aspen, the longest shoots are found arising from the middle regions of the parent shoots (Fig. 11). The low R^2 is an indication of the variability in daughter shoot length that occurs along crooked aspen parent shoots. Part of this variation is a gravimorphic response. Although shoots are produced at all locations around major parent shoots of the crooked aspen, a larger proportion is produced from the top locations (31%) compared with the sides and bottom locations (approximately 23% for each) (χ^2 test of independence of frequency of shoots versus location around parent: $\chi^2 = 11.85$, $P = 0.0079$, $n = 724$ shoots). Moreover, despite considerable variation in length, the longest shoots tend to develop from the upper surface, often near the bend of the parent

Fig. 12. Sympodial growth in the main stem of a wild-type *Populus tremuloides* specimen. The shoot on the left (D) is the most distal lateral below the aborted terminal (arrow) but the replacement shoot (R) is actually located one node below D.

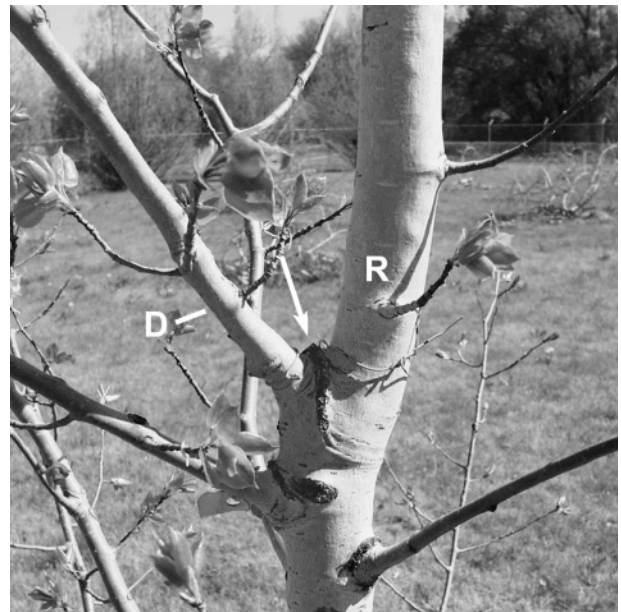
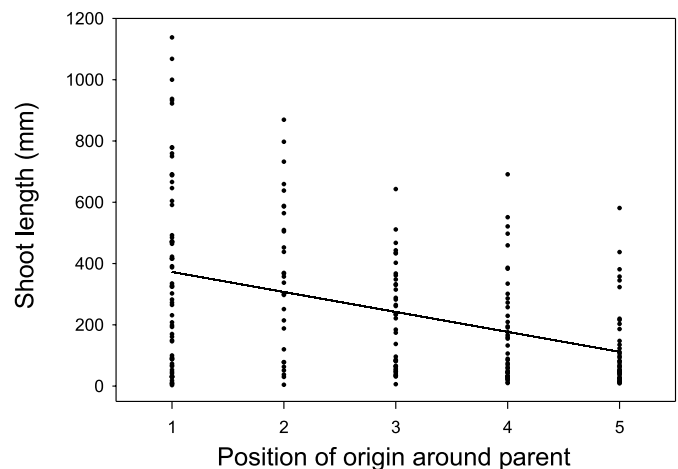


Fig. 13. Relationship between daughter shoot length and position of origin around the parent of crooked *Populus tremuloides* (see Table 1 for an explanation); $Y = 437.18 - 65.14X$, where Y is the length and X is the position of the origin ($P < 0.0001$, $R^2 = 0.16$, $n = 224$ daughter shoots).



(Fig. 13). Thus, if only those shoots arising from the upper side of parent shoots were considered in the regression analysis of length in relation to location along the parent, the R^2 improved to 0.24.

Once a pattern of decreased vigour was established at the distal end of curved parent shoots, there was a tendency for the loss of vigour to accelerate, and in a sample of 15 relay shoots, this was manifested in one of two ways after 3 years. (i) Nine of the relay shoots had continued to develop a yearly terminal shoot over the 3-year period examined. However, the amount of extension decreased significantly from year to year (Fig. 14A). In comparison, in the normal

Fig. 14. Plots of means and standard errors of extension growth increments over three successive years in crooked and wild-type *Populus tremuloides*. (A) Length of relay shoots (increment 1) and subsequent terminal extension increments of relay shoots. Means were significantly different based on ANOVA ($P < 0.0001$, $n = 9$ relay shoots). (B) Length of main stem increments in wild-type trees. Means were not significantly different at $P = 0.05$ ($P = 0.08$, $n = 4$ trees). (C) Length of extension increments in a branch arising from the first increment in Fig. 14B. Means were not significantly different ($P = 0.93$, $n = 4$ branches).

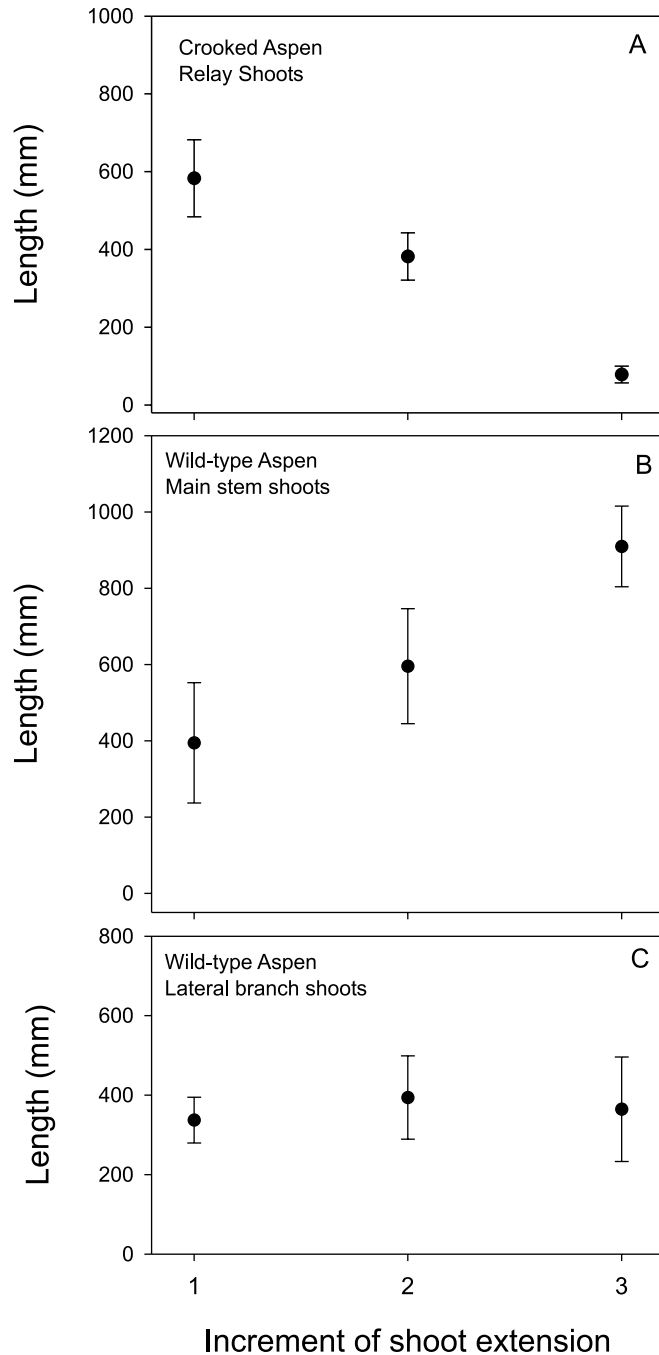
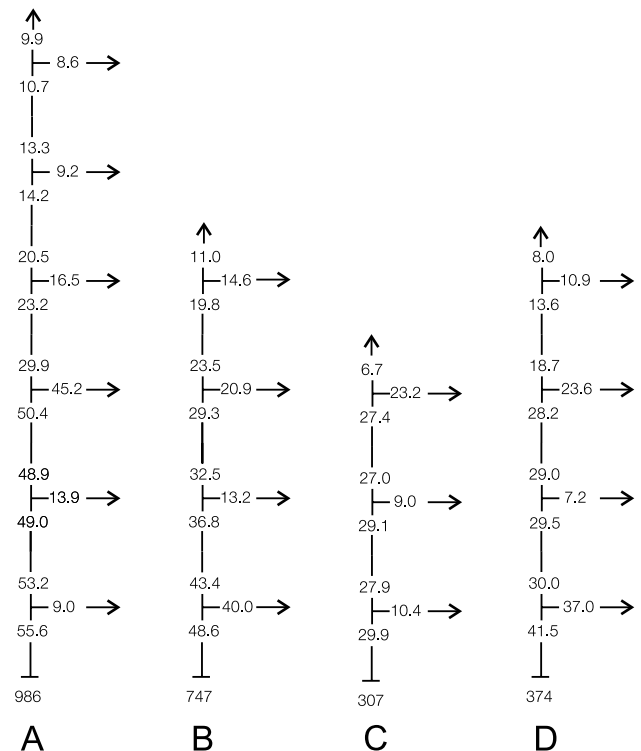


Fig. 15. Photograph showing decline in vigour (D) of a crooked *Populus tremuloides* parent relay shoot as indicated by reduced diameter distal to two daughter relay shoots (arrows). Note how the wide divergence angles of daughter shoots result in the relay axes growing back toward the middle of the tree.



Fig. 16. Diameter relationships of four 1996 major relay shoots (depicted as vertical lines) and their lateral daughter shoots (horizontal arrows to the right) of crooked *Populus tremuloides* as they appeared in 2000. Each 1996 shoot comes from a separate tree. The numbers inserted in the vertical lines indicate the diameters (mm) of the 1996 parent relay shoot measured just distal and proximal to the lateral. The number in the horizontal line refers to the diameter approximately 1 cm from the base of the lateral. The numbers below the horizontal bars, which depict the base of each parent relay shoot, indicate their lengths (mm). The tips of the parent relay shoots are indicated by arrows. Note that the shoots depicted in the diagrams are not drawn to scale.



wild-type aspen, there was no significant difference in the amount of extension growth between years for either the main stem leader or the branches (Figs. 14B and 14C). In fact, in contrast with the crooked aspen, there was a trend for the extension growth of the main stem to increase over time, although there was considerable variability. (ii) In the other six curved parent relay shoots, by the third year, the tips of the original relay shoots had actually died back, with only a mean $78.3 \pm 4.6\%$ of the shoot still present. The time when dieback occurred, and therefore the amount of extension growth achieved by the axis prior to this, was not recorded.

After 5 years, the decline in vigour of the portion of the original relay shoot distal to the junction with the daughter relay shoot was often very apparent (Fig. 15). In three of four cases (Figs. 16A, 16C, and 16D), diameter growth of the parent distal to the relay shoot declined significantly compared with that of both the relay shoot and the portion of the parent shoot just proximal to the junction. In one case, however, there was little decline in diameter because there were a number of vigorous laterals distal to the junction (Fig. 16B). Observations throughout the crowns of the young crooked aspen trees revealed that the original axis frequently died right back to the junction with the relay shoot (Fig. 9). In some cases, this occurs because a relay shoot is near the tip of the parent (Fig. 16C).

Angle of divergence of lateral shoots

On the leading parent shoots of normal wild-type aspen, there was no significant relationship between divergence angles of lateral shoots and their location along the parent. The mean angle of divergence was $56.23 \pm 1.11^\circ$ (Fig. 17). However, a lateral shoot that replaces an aborted terminal may bend in the direction of growth such that there is a very small divergence angle. In the crooked aspen, the divergence angles of daughter shoots on the curved relay shoots were generally greater than in the wild type. There was a more distinct pattern in that the divergence angles were less for laterals near the tip and greater for those near the middle (Fig. 17). Moreover, in the crooked aspen, the divergence was sometimes more than 90° and the result was that such daughter shoots often bent back away from the direction of growth and grew towards the centre of the tree (Figs. 6 and 15).

Relationship of shoot diameter to length

In an effort to assess whether the shoots of crooked aspen may not be as strong as those of wild-type aspen, thus contributing to their pendulous behaviour, the relationship between basal diameter and length of current-year shoots was examined. As expected, there was a close relationship between length and diameter, but as the shoots became longer, the wild-type aspen shoots had an increasingly smaller diameter than comparable-length crooked aspen shoots (Fig. 18).

Discussion

Populus tremuloides is one of the most common deciduous trees in North America and is generally recognizable as having an excurrent crown architecture with a single main stem, particularly in early stages of development (Millet

et al. 1999). The architecture consists of an orthotropic, monopodial main axis bearing subordinate lateral first-order axes in a more or less acrotonic pattern. Like other *Populus* species and hybrids (e.g., Burk et al. 1983; Ceulemans et al. 1990), *P. tremuloides* conforms to the architectural model of Rauh (Hallé et al. 1978) in which all shoots are considered orthotropic even though many shoots are oriented at an oblique angle with respect to gravity. For example, in the

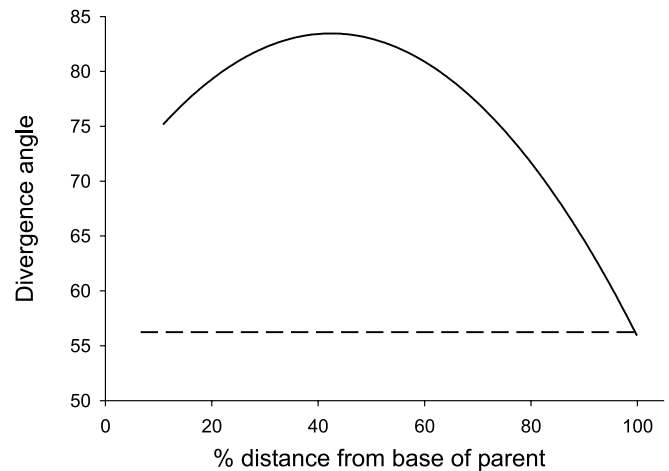
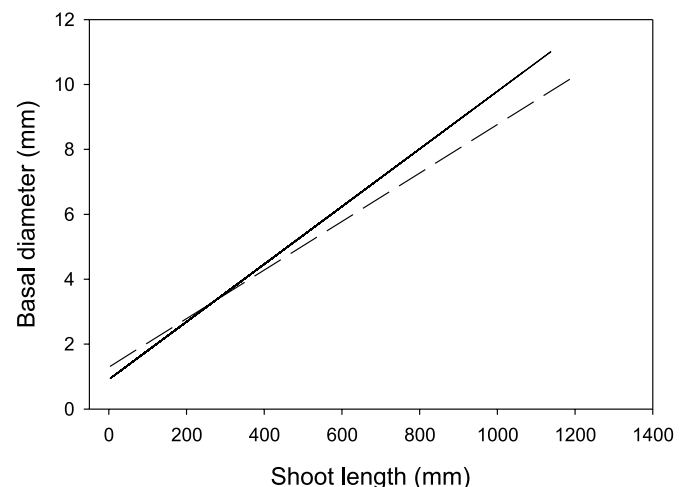


Fig. 18. Relationship between basal diameter (Y) and length (X) of current-year shoots of crooked *Populus tremuloides* (solid line: $Y = 0.91 + 0.0089X$; $P < 0.0001$, $R^2 = 0.84$, $n = 144$ shoots formed in 1997 and 1998) and wild-type *P. tremuloides* (broken line: $Y = 1.29 + 0.0075X$; $P < 0.0001$, $R^2 = 0.95$, $n = 138$ shoots formed in 2001). Slopes were significantly different at $P < 0.0001$.



et al. 1999). The architecture consists of an orthotropic, monopodial main axis bearing subordinate lateral first-order axes in a more or less acrotonic pattern. Like other *Populus* species and hybrids (e.g., Burk et al. 1983; Ceulemans et al. 1990), *P. tremuloides* conforms to the architectural model of Rauh (Hallé et al. 1978) in which all shoots are considered orthotropic even though many shoots are oriented at an oblique angle with respect to gravity. For example, in the

present study, using 90 minus the angle of termination as an indirect measure of elevation for order 1 laterals, the mean elevation angle was calculated to be approximately 41°. In contrast with wild-type aspen, the architecture of individuals of the “crooked” clone is sufficiently different to warrant affiliation with other models characterized by mixed orientation of shoots in which the same meristem gives rise to both upright and horizontal to pendulous components of the structure. In this case, a single main stem is not recognizable and the plant may take on a shrubby appearance. Büsgen and Münch (1929) provided an early explanation for woody plants that develop from axes that change orientation. They attributed the architecture of *Sambucus nigra* to branches becoming pendulous under their own weight, presumably due to lack of strength to keep them upright. This is the model of Champagnat (Hallé et al. 1978). Although the architecture of the crooked aspen appears to superficially resemble Champagnat’s model, the relay shoots of crooked aspen actually had a greater diameter than comparable wild-type shoots, suggesting that lack of strength may not be the controlling factor. However, it should be pointed out that the diameter was measured at the base of the shoot without regard to taper, and strength may also be related to factors other than stem thickness such as the presence or absence of reaction wood. In any event, further research would be necessary to determine a possible role for stem thickness and other anatomical factors in crown architecture development in the crooked aspen.

Another possible explanation for the bending of shoots is that it is a more active, physiological process. In plants, there is typically an inherent tendency for shoots to grow orthotropically upwards in response to the gravitational stimulus. Many of the relay shoots of crooked aspen appear to exhibit such a gravitropic response, at least initially. Preliminary investigations of the bending behaviour indicate that the current-year relay shoots, which ultimately become pendulous, may initially grow with an upright to oblique orientation and then bend downwards at a distance from the tip as the season progresses. This type of development resembles the model of Mangenot (Hallé et al. 1978) in which the apical meristem first produces an upright basal portion followed by distal horizontal part. However, in Mangenot’s model, there appears to be an abrupt change in orientation of the growing tip rather than a more gradual bending down of the shoot as was observed in the present study. Moreover, a preliminary experiment in the greenhouse with young plants that were turned upside down revealed that the tips of shoots initially exhibited gravitropic behaviour but eventually bent downward (data not shown). Although inability to retain orthotropic growth because of lack of strength could contribute to such behaviour, it is possible that the bending down of shoots may be a gravi-epinastic effect (Hart 1990) in which endogenously controlled differential growth acts to force a branch to grow downwards. A comparison of crooked aspen with normal aspen grown under reduced gravity may be useful in furthering our understanding of the response. The observation that current-year shoots also frequently bend in the horizontal plane also lends support to the notion that the bending is an active process and not just a function of stem strength. Propagation experiments (data not shown) have revealed that the crooked trait is under genetic control. Given

that genetic control of gravitropism has been widely studied in recent years (see Fukaki et al. 1996; Chen et al. 1999), it may be reasonable to postulate that the bending down of shoots in crooked aspen results from a change in gene expression that manifests as increased auxin transport to one side of the shoot. Earlier work by Lyon (1967) indicated that differential auxin transport played a role in the gravi-epinastic behaviour of shoots. Other hormones may also be involved as has been shown in other studies where GA₃ applied to apical buds of weeping Japanese cherry inhibited bending of branches (Nakamura et al. 1994), and a role for ethylene has been demonstrated in the gravitropic response of tomato (Madlung et al. 1999).

Shoots that are bent towards the horizontal typically exhibit gravimorphic physiological differences between the upper and lower sides (Kaldewey 1967). In bent stems, more shoots arise from the upper side and occasionally no shoots develop on the lower side (Wareing and Nasr 1961; Audus 1969). In the crooked aspen, although the proportion was somewhat less, lateral shoots were freely produced from buds on the lower sides of parent shoots. Nevertheless, daughter shoots arising from the upper surface tended to be longer than those arising from the lower side, supporting the notion of gravimorphism. Differential extension growth of lateral shoots arising from the upper and lower sides of branches of trees is not uncommon. However, in certain species of *Fraxinus*, the shoots arising from the lower half of parent shoots are typically longer than those from the upper half (*Fraxinus pennsylvanica* (W.R. Remphrey, unpublished data), *Fraxinus americana* (Millet et al. 1999)). In such cases, the increased growth of lower shoots appears to play a role in controlling how the crown expands outwards.

Besides the differential growth of shoots arising from the upper and lower surfaces of a bend, Wareing and Nasr (1961) reported that another gravimorphic consequence of displacing shoots from a vertical to a more horizontal orientation in various fruit tree species is a reduction in the extension growth of horizontally trained shoots compared with upright shoots. Quantitative analysis of the crooked aspen major axes also revealed, in most cases, a dramatic decrease in subsequent extension growth of that axis, and eventually the terminal shoots of many of these axes were dead, sometimes back to the relay shoot. This is in contrast with normal aspen, which conformed to the pattern usually reported for trees whereby leader growth typically increases during early stages of development (e.g., Daniel et al. 1979) followed by a gradual decline. Branches often begin to show this decline relatively early in their development, a phenomenon known as ageing (Moorby and Wareing 1963).

In normal aspen, the distal lateral shoots tend to be longest and they become progressively shorter towards the basal end. This pattern is known as acrotony (Champagnat 1978) and is common in many tree species, especially those exhibiting an excurrent form. In the crooked aspen, instead of acrotony, there was a variable but recognizable pattern of mesotony whereby the longest, most vigorous shoots arose from more central regions of the parent shoot. Wareing and Nasr (1961) showed that displacement to the horizontal reduced the growth of all lateral shoots but the most distal laterals showed the greatest proportional decrease. They suggested that the normal apical control resulting in the

acrotonous pattern was only manifested when the parent shoot occupied a more vertical position. In the tortillard beeches, Thiébaud et al. (1993) attributed part of the twisting response to diminishing apical control and an increase in sympodial growth leading to forks in the branching system. In the crooked aspen, the growth of the axis is monopodial for a time but the leading shoot of the axis repeatedly arises laterally as a relay shoot (see Prusinkiewicz and Remphey 2001).

One of the responses to a reduction in vigour of daughter shoots arising from distal regions of parent relay shoots was an overall reduction in stem diameter increment of the parent relay shoot distal to the daughter lateral relay shoots in the vicinity of the bend. This reduction is consistent with the pipe model theory (Shinozaki et al. 1964) that has been used frequently to show that diameter growth at a given location is correlated with the leafy shoot growth distal to that point (e.g., Robichaud and Methven 1992). This reduction in diameter growth or even dieback to the main lateral relay shoot accentuates the crookedness of the tree. This effect is exacerbated by the maintenance of a wide divergence angle for the replacement lateral shoot. In many trees, when the vigour of an upright leading shoot is reduced or the terminal is lost, the uppermost laterals assume a more upright orientation when apical shoot vigour is reduced (Remphey and Powell 1984; Wilson 1998). Typically, this results in a narrower divergence angle than would normally be the case. This response is shown in normal *P. tremuloides* by the formation of bayonet joints along major axes (Fig. 12). Conversely, in the crooked aspen, vigorous relay lateral shoots arising from horizontal portions of the previous year's shoot tend to have wide divergence angles, often exceeding 90°. Overall, such shoots tended to have a wider divergence angle than any comparable shoots of wild-type aspen. One of the consequences of this wide divergence angle in crooked aspen is that the direction of growth of the relay shoot may be completely opposite that of the parent. This type of development appears to keep the crown somewhat confined as opposed to reports in other species such as the twisted larch described in the introduction in which the plant spreads as a result of the reorientation.

In conclusion, the crooked form of the aspen clone growing near Hafford, Saskatchewan, results from several developmental processes that appear to be initiated by the production of shoots that curve during development. Besides the curves themselves, the formation of pendulous shoots sets in motion subsequent gravimorphic responses that include the development of vigorous relay shoots at or near the bend of parent shoots and a decline in vigour of the curved shoot as it develops further, leading to ultimate dieback, coupled with the retention of a wide divergence angle in the relay shoot. Taken together, these processes appear to play a significant role in the formation of the extreme crooked morphology of the trees. A next step will be to develop a visual simulation model that will be used to test these hypotheses.

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